THE BIOSTRATIGRAPHY, PALAEOECOLOGY AND TAXONOMY OF UPPER CRETACEOUS (CONIACIAN TO LOWER MAASTRICHTIAN) OSTRACODA FROM THE CHALK OF EAST ANGLIA.

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Volume 1 - Introduction, Systematic Taxonomy

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ABSTRACT

The thesis is based on 205 sediment samples supplied by the British Geological Survey from the Trunch Borehole and various outcrop localities in Norfolk and Suffolk. At least 80,000 ostracod specimens were recovered, belonging to 151 species and 53 genera. These are fully illustrated and described in a large systematic taxonomy chapter. Seventeen species and 1 subspecies were described as new. A stepped pattern of origination and extinction occurs throughout the Upper Chalk of East Anglia and the Ostracoda thereby display high biostratigraphical potential. The large number of Lazarus taxa in the Santonian and Lower Campanian is a distinctive feature.

An analysis of the percentage of filter feeding platycopid Ostracoda, as a measure of palaeoxygen levels, reveals large variations in the amounts of dissolved oxygen in the Upper Cretaceous of East Anglia. High percentages of platycopids equate to low oxygen and *vice versa.* This is confirmed by the fact that high levels of platycopids are always associated with low species diversity. Using this technique, it was shown that the Coniacian was a time of low to very low oxygen, except for the upper part (*coranguinum* Zone) which was better ventilated. The Santonian and Lower Campanian were low to very low in dissolved oxygen, while the Upper Campanian and Lower Maastrichtian had much higher levels of dissolved oxygen. The term "Kenoxic Event" can be used to describe such periods of lowered oxygen, when instar-brooding platycopids display a preferential survival potential compared to podocopids. Notwithstanding these general trends, oxygen levels appear to have fluctuated rapidly throughout the interval of study. These fluctuations are thought to be due to the Oxygen Minimum Zone and its migrations onto the continental shelf and subsequent retreat to the continental slope; low oxygen levels on the continental shelf being extremely deleterious to all other Ostracoda other than platycopids resulting in low diversity. High diversity and high oxygen are associated with the retreat of the OMZ onto the continental shelf. This in turn is related to sea level fluctuations and the technique shows good potential for use in sequence stratigraphy. A model showing the position of the Oxygen Minimum Zone during the Upper Cretaceous in East Anglia was produced from platycopid data generated by this study.

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- Klondike Kate is mentioned here just for being herself.

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90 TF TG 10 20 30

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0 10 km

0 10 miles

Scolt Head Island

Blakeney Point

Blakeney Harbour

Morston

Cley

Weybourne Hope

West Runton

Cromer

Overstrand

Sidestrand

Trimingham

Mundesley

Trunch Borehole

North Walsham

Horstead

Wroxham

Broac

Thorpe

Whitlingham

Trowse Newton

Bramerto

Burnham Overy

Burnham Market

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Little Walsingham

Houghton St Giles

Holt

Melton Constable

Saxthorpe

Blickling

Aylsham

Heydon

East Rudham

Ryburgh

Helhoughton

Guist

County School

North Elmham

Reepham

Alderford

Litcham

Swanton Morley

Attlebridge

Frettenham

Newton-by-Castleacre

East Dereham

Taverham

Drayton

St Faith's Airfield

Costessey

Cotton

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Bowbrigh

Eaton

Cringleford

Harford Bridge

Hethersett

Keswick

Calstor St Edmund

Ashill

Saham Toney

Watton

Scoulton Mere

Hingham

Seamere

Wymondham

Stoke Holy Cross

Newton Flotman

Flordon

Stow Bedon

Thompson Water

Attleborough

Tacolneston

Tharston

Forncett

Quidenham

High Starlings

East Harling

Tivetshall

Burston

NORFOLK

SUFFOLK

Diss

Scole

Map location

TG / TM

TF TG 10 20

B.lanceolata Zone

Paramoudra Chalk

'Beeston Chalk'

Cotton sponge Bed Horizon

'Weybourne Chalk'

'Eaton Chalk'

Basal *mucronata* Chalk

Gonioteuthis Zone

Marsupites Zone

Uintacrinus Zone

M.cor-anguinum Zone

Zone of Belemnitella mucronata

Upper Senonian

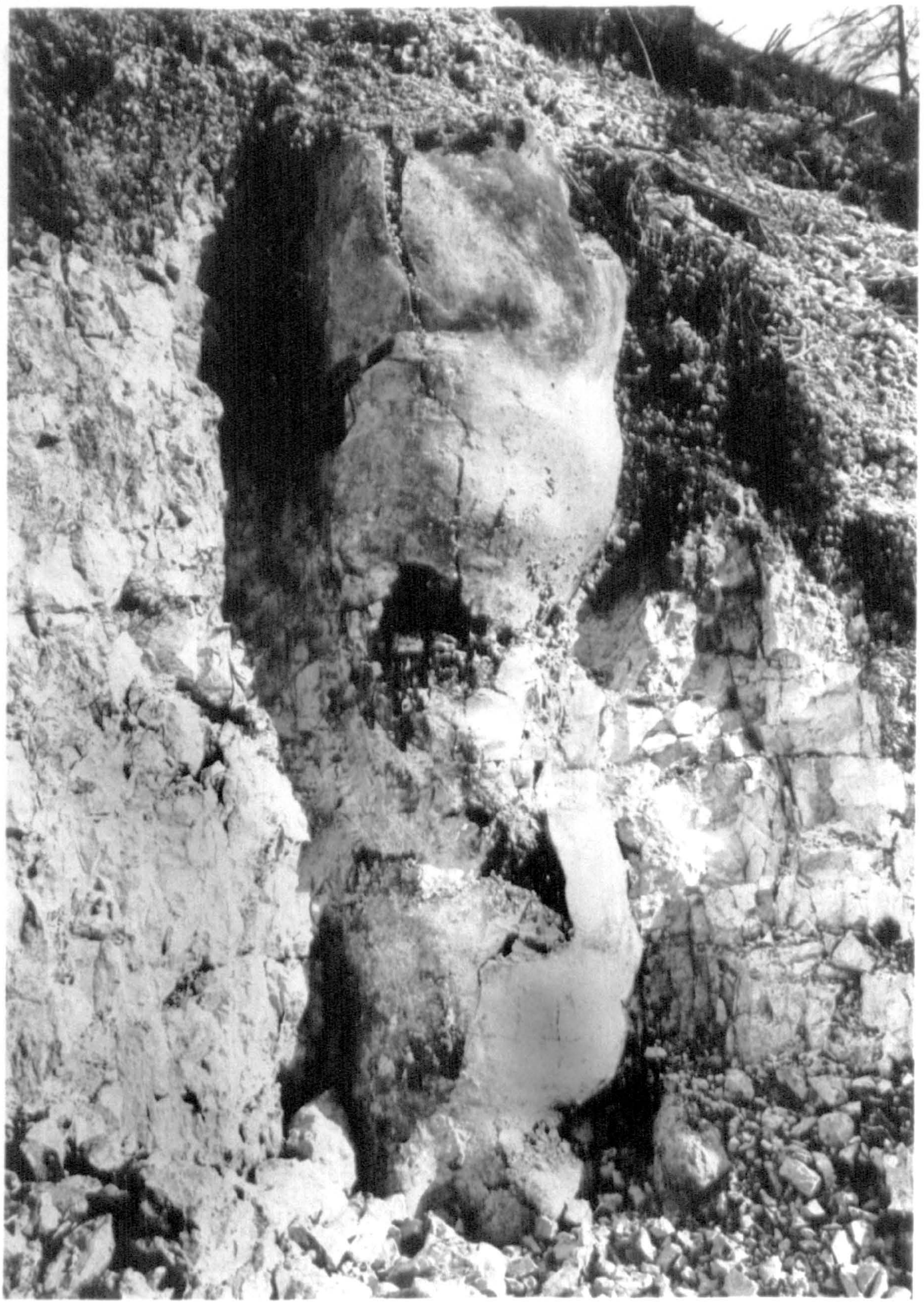
M. Senonian

Maastrichtian

1: Chalk pit, Keswick, exposing gently folded chalk – BGS photograph A11125

2: Caistor St. Edmunds, general view of chalk pit – BGS photograph A11129

3: Whitlingham Pit, general view of chalk face with Paramoudra – BGS photograph A11128



4. Whitlingham Pit, chalk section with 2m long Paramoudra – BGS photograph A11127

CHAPTER 1

INTRODUCTION, AIMS AND METHODOLOGY

Introduction and aims of this study:

The Upper Chalk Ostracoda of the British Isles have not been studied since Jones and Hinde published their monograph on the subject in 1890, and this classical work is almost entirely taxonomic in nature. The material from the Trunch Borehole and outcrop samples from various localities, on which the present study is based were provided by the British Geological Survey. The ostracod assemblages were studied using standard micropalaeontological techniques. The zonation of each borehole and outcrop will be followed by a basin wide correlation.

The palaeoecology of the various faunal assemblages will be used in this study to recreate, wherever possible, the palaeoenvironments as a dynamic function of the evolution of the basin. It is known, for example, that at certain horizons, filter feeding platycopid ostracods dominate and this is clear evidence of dysaerobia. The importance of these so-called Kenoxic Events is fundamental to the understanding and application of Sequence Stratigraphy.

In this thesis, six research aims will be addressed and these are as follows:

1) To identify, illustrate and analyse the ostracod fauna of the areas under study. To fully describe all new taxa and to compare and contrast ostracod assemblages separated in time and space.

2) To analyse the biostratigraphical distribution of the Ostracoda of the Trunch Borehole and of each of the outcrop localities. To compare composite range charts for all outcrop localities with those drawn for the Trunch Borehole. To prepare a range chart for the Coniacian to Lower Maastrichtian of East Anglia based on both the Trunch borehole and the outcrop samples.

3) To attempt the production of an ostracod zonal scheme for the Upper Cretaceous of East Anglia.

4) To attempt to employ the percentage of filter feeding specimens in the ostracod assemblages as a tool in reconstructing palaeo-oxygen levels, the detection of kenoxic events and, thereby, to determine the relative sea level and position of the Oxygen Minimum Zone within a sequence stratigraphy framework.

5) To attempt palaeoenvironmental reconstruction based on the application of palaeoecological principles using the Ostracoda.

6) To prepare for publication those parts of this study which are considered to be of particular value.

Methodology

The samples were supplied by the British Geological Survey as prepared residues. The method by which the raw rock samples had been treated is as follows "soaked in white spirit to disaggregate the chalk as far as possible, boiled in sodium hexametaphosphate and washed through a 200 BS (c.75 micron) sieve" [*pers.com.* Dr. Ian Wilkinson, 1st and 19th October 1996, see also Wilkinson, 1988a, MS]. Dr Ian Slipper (MS, 1997) has carried out a large and extensive study on the

effects of processing on assemblages vs. different processing methods. The white spirit method is, in his opinion, not really suitable for use with pure chalk rock [*pers. com.* ISO'97] but it is a standard processing method which is widely used. In the present study, the majority of specimens were well preserved or moderately well preserved.

Picking. In the case of the Trunch Borehole, samples were picked every 5 metres. All of the outcrop samples identified in the BGS stratigraphical log to be of Coniacian to Lower Maastrichtian age were picked for ostracods, although some proved to be barren. Each residue was placed on a picking tray and examined under a stereoscopic binocular microscope. A fine sable brush was used to transfer ostracod specimens from the picking tray to multi-celled grid square slides. These slides had been coated with a solution of gum tragacanth and allowed to dry. Detailed notes were kept for each sample, listing the appearance of the sediment and the nature of the biogenic component. Counts to determine platycopid and podocopid percentages were also made at this stage. Wherever possible, 301 specimens were picked out of each sample. This is a statistically accepted count size used by many authors. In some samples, especially those of the Trunch Borehole, this was not possible due to low ostracod abundance or grain size. In such cases, 100 specimens were picked for each sample.

Sorting. Specimens were first sorted within each sample slides, and then for selected species. Each species slide, therefore, contained all the representatives from each sample in which that species occurred. This method allows easy comparison of material and a quick way to count the number of individuals of any one particular species found in each sample. By examining each species slide, the range of variation allowed for a species could be determined. Detailed notes concerning population structure (sexual dimorphism and ontogeny) were made at this stage.

Further preparation of specimens

Cleaning. Although the method by which the samples were prepared commonly results in clean specimens, in the present study many specimens were found to contain calcareous matrix which completely or partially obscured details of ornament or internal features such as the hinge or muscle scar configuration. Such specimens needed to be cleaned to remove extraneous material. This cleaning may be done manually, chemically or mechanically (Sohn, 1961, p. 67-68).

Manual cleaning, the method used in the present study, is a time consuming method and constraints during the course of research meant that it could not be carried out on all specimens. The specimen to be cleaned was placed on a clean glass slide and held in place with water. The adhering matrix was very carefully removed under the microscope with a fine dissecting needle and the cleaned specimen returned to the assemblage slide. Chemical methods were also considered whereby matrix was removed from individual valves by soaking in hydrogen peroxide in a concave glass slide. The process is carefully monitored and loosened material removed with a dissecting needle. This method was tested using several species and a 5% solution of hydrogen peroxide; it is adequate for robust genera such as *Amphicytherura, Cythereis, Cytherella, Bairdoppilata, Cytherelloidea* etc., but may cause damage to more fragile, thinner shelled taxa. The manual method is probably better, allowing the worker to control the speed of the cleaning process and avoiding

unnecessary damage. Sohn (1961) discusses cleaning by ultrasonic vibration. This method, however, involves the use of complex and expensive equipment and, although suitable for certain microfossil groups (e.g foraminifera), is not really suitable for use in ostracod studies due to the tendancy towards breakage.

Staining. The use of a stain, especially in reticulate genera, brings out fine details of the ornament that could not otherwise be seen. Malachite green dissolved in alcohol is considered to be most suitable for use in ostracod work due to the rapid speed at which it dries and was used extensively by Pokorny (1967c) in research into the Upper Cretaceous Ostracoda of Bohemia. In this study, blue food colouring provided good results and is easily removed by washing in water.

Illustration. Preparation of the stubs used in Scanning Electron Microscopy (SEM) employed the standard method. Specimens were mounted on a small square of double-sided tape placed on an aluminium stub. The edges of the tape were painted with a silver dag paint to ensure a good electrical conductivity and then left to dry. Care was taken to ensure that this edging paint was thoroughly dry, otherwise it might have evaporated during the coating procedure and caused unequal coating and expensive damage. A sputter coater was used with a 120 second setting to coat the stubs with 100 angstroms of gold alloy. The process was repeated with the stubs laid at an angle. This ensured that the edges of each specimen were properly coated, an essential consideration in large genera such as *Bairdoppilata* and *Cytherella*.

Whittaker & Hodgkinson's (1990) method for making plates using a black background was adopted in the preparation of plates 1-27 in the present study. All illustrated specimens (including holotype and paratype material) have been deposited with the BGS - catalogue numbers MPK 11272 to 11843.

British and European Cretaceous Ostracod research - A summary of the last 110 years;

Neale, writing in 1978, stated that "in Britain, the Upper Cretaceous faunas are not yet known in sufficient detail to allow the development of a zonal scheme". An overall view suggests that the lower half of the Upper Cretaceous is well served from the point of view of taxonomy, stratigraphy and stratigraphical distribution of species but suitable exposures are limited geographically. Jones and Hinde's monograph on the Cretaceous ostracods of England and Ireland (1890) is "doubtless the best single paper that has been published on Cretaceous Ostracoda" (Alexander 1929). The work is a compilation of all the important studies in that field up to 1890 and clears up synonymy and demonstrates, by the use of various tables and diagrams, vertical and horizontal distribution though the Cretaceous of Europe. In the current work, the author has referred to Jones and Hinde's original descriptions and plates. Although in many cases, the species names have changed, some of the species seen in the current work appear to be almost identical to those in the earlier monograph.

Little work has been carried out on Upper Cretaceous ostracods of East Anglia in more recent times and the literature is very sparse. Albian, Cenomanian and Turonian assemblages have been relatively well documented in the area (Wilkinson & Morter, 1982; Wilkinson, 1988a MS, 1988b; 1990). This thesis on the Ostracoda from the Coniacian to Lower Maastrichtian of the area is

important, therefore, in that it will help to increase the knowledge of this interval.

Most of the early work on Cretaceous ostracods in Britain and Europe (e.g. Triebel, 1938, 1938b, 1940, 1941, 1950; Sylvester-Bradley, 1941, 1948) was largely taxonomic. It was not until the 1950's and ' 60's that a number of stratigraphically useful papers began to appear (e.g. Mertens 1956; Oertli, 1958; Neale, 1960, 1962; Herrig, 1966, 1967a, b, c; Gründel 1966, 1968a, 1968b, 1969a, 1969b, 1970a, 1970b). Kaye, 1964a, published a revision of British Marine Cretaceous Ostracoda, working on the specimens of Jones (1849), Jones & Hinde (1890), Chapman & Sherborn (1893) & Chapman (1898). Kaye attempted to refigure and redescribe as many of the original species as possible and interpret them within the existing classification of the 98 specific units considered; 55 were retained as valid species. The distribution of ostracods through the British Lower Cretaceous was documented by Neale (1973) and five years later a stratigraphical range table for the entire British Cretaceous (Neale 1978) was produced, which is comparable with those published by Damotte (1971a) for the Cretaceous of France. The British range charts have recently been revised for publication and will appear in a forthcoming BMS atlas. The Cretaceous zonation has, however, been made available via the World Wide Web (seen by the present author in May 2000 and discussed in a later section of this thesis).

Pokorny published an extensive series of studies (taxonomy and biostratigraphy) of ostracod genera from the Cretaceous of Bohemia; covering *Phacorhabdotus* (1963), *Oertliella* and *Spinoleberis* (1964), *Cythereis* (1967a), Platycythereis (1967b), *Curfsina* (1967c), *Bairdia* (1975a, 1975b), *Bairdoppilata* (1977) and *Mosaeleberis* (1978). Deroo (1966), and Bless (1988), have undertaken major taxonomical and biostratigraphically based studies of Upper Campanian and Lower Maastrichtian in Holland.

Babinot (1980) produced a detailed study of both marine and freshwater ostracod faunas from the Upper Cretaceous of Provence, describing and illustrating 174 species. Of these, there were 53 Cenomanian, 18 Lower to middle Turonian, 25 Upper Turonian and Coniacian, 57 Santonian and 21 from the Upper Senonian). 27 of the species are new and two new genera are erected. Babinot also includes a useful and enlightening discussion on the choice of classification, illustrating the difficulties faced in choosing between the numerous existing nomenclatures. His work is also biostratigraphical and palaeoecological in nature.

King (1968, MS) studied selected ostracod species from the Upper Chalk of the British Isles in a largely taxonomic treatment. 128 species are described in detail, belonging to 39 genera and subgenera and restricted, with the exception of the genus *Cytherelloidea*, to the Cytheracea. King concluded that "although of limited value in long distance correlation, the ostracods are useful in local stratigraphy. A series of distinct faunas can be recognised in Norfolk." Many species listed in the 1968 thesis also appear in the Santonian to Lower Maastrichtian assemblages of East Anglia and the stratigraphical ranges of these are very similar.

Several other more recent doctoral studies have been those carried out by Johnson (1996, 1997a, 1997b, 1997c) and by Slipper (1996, 1997) on the Ostracoda of the Turonian and Cenomanian interval. Some species in the Turonian or Cenomanian of Southern England, also appeared in the later intervals covered by this current work. Johnson (1997a, p. 79) carried out an

extensive study of ostracod biogeography during the Cenomanian - Turonian Oceanic Anoxic Event in Europe. Podocopid ostracods from the Plenus Marls at English localities show stepped patterns of extinction through an interval marked by a "strong positive carbon stable isotope excursion corresponding to the Cenomanian-Turonian Anoxic Event." Platycopids show no such extinction. Johnson also noted the virtual absence of *Cytherelloidea* from English sections and provides a detailed study of the global palaeobiogeography of this genus, concluding that this "challenges the commonly held belief (e.g. Sohn, 1964) that it is a warm water indicator." Few, if any, other workers support this statement. Most continue to accept the genus as a thermophilic indicator (Schudack, 1999, 2000 p. 109; this thesis, chapter 4).

French workers have carried out many useful studies of Cenomanian ostracods. Babinot (1970, 1971); Colin (1973a, 1973b, 1974a, 1974b); Damotte (1971, 1976); Damotte & Grosdidier (1963) and Donze (1972) have all shown how Cenomanian ostracods can be important both stratigraphically and palaeoecologically. Babinot *et al.*, (1978) summarise the results of this work, revealing ostracod provincialism during the French Cenomanian. German Cenomanian ostracods have been studied by such authors as Gründel (1966) and Mertens (1956). Gründel produced a range chart showing the distribution of 87 species through the German Albian. Mertens (1956), recognising the usefulness of ostracods in stratigraphical determination, produced a range chart for the Upper Albian and Late Cenomanian. Weaver (1982) produced a monograph of Ostracoda from the British Lower Chalk and Cenomanian Plenus Marls of Southern England, describing 117 species and subspecies (58 new) in a taxonomical and biostratigraphical context.

The British Cretaceous; depth, sea level and biostratigraphy of the Chalk Sea.

The Upper Chalk is a white micritic limestone, formed in the late Cretaceous seas as low Mg-Calcite (Hancock, 1975). While the Chalk of Southern England is soft because of the concentration of silica into flint nodules and bands, in Northern England the silica is distributed throughout the sediment and the rock is generally much harder. During the late Cretaceous, there was little land in Northwest Europe available for erosion because of the high eustatic sea levels (Montford, 1970). A non-seasonal climate meant little erosion and, therefore, very little terrigenous input; the Chalk is generally pure because of this low level of terrigenous contamination. British Chalk contains only a small quantity of clay minerals and clay-grade detritus, which is mostly quartz. Throughout much of the Coniacian, Santonian and Campanian stages of Southern England, such materials make up less than 1% of the Chalk rock; a specific unit within the Chalk itself (Montford, 1970). Neale (1978) provides a hypothetical reconstruction of Cretaceous palaeogeography and notes the progressive extension of marine influence, stating that "marine early Cretacous rocks are restricted to Yorkshire, Lincolnshire and East Anglia. Elsewhere, the rocks are of Wealden Facies and are found only in Southern England." Gradual encroachment by the sea in Southern England during the Aptian led to the development of marine conditions between northern and southern areas and the rapid expansion of shallow shelf seas, and hence the widening in the areas of outcrop available for study in the Albian. Further expansion took place during the Upper Cretaceous with widespread deposition of the Chalk.

Conditions of deposition:

1- Salinity. The widespread abundance of macrofossil groups such as echinoids and brachiopods indicates that the Chalk Sea was of normal salinity (c.35 ºoo) since such organisms cannot flourish in lower salinities. The biostratigraphical logs of the Trunch borehole (Appendix 1) list a wide diversity of echinoids and other macrofossils. It can be inferred, therefore, that the sediments of the Trunch Borehole were deposited in normal marine conditions. A University of Durham website page ([http://www.dur.ac.uk: 80 report 97/res-int 97.html]) seen by the current author in 1999, on the sequence stratigraphy of a pelagic chalk succession of the Anglo-Paris Basin (Coniacian to Campanian) is interesting. It suggests that, in the Anglo-Paris Basin, salinity stratified conditions existed linked to the initiation of an upwelling system during the late Santonian, breaking down to a thermally stratified ocean in the Lower Campanian. A sequence stratigraphy of the Anglo-Paris Basin was later published by Grant *et al.*, 1999.

2) Depth of sedimentation. The depth at which the Cretaceous chalk was deposited has been widely studied and debated (Hume, 1894; Jukes-Brown and Hill, 1904; Rowe, 1908, Neaverson, 1928; Barr, 1962: Burnaby,1962; Nestler,1965; Håkkanson et al., 1974; Bennison & Wright, 1975; Hancock,1975; Jenkyns, 1986; Puckett,1991, 1992, 1996). Rowe (1899, 1901, 1902, 1904, 1908) published 5 papers entitled " The Zones of the White Chalk of the English coast", each describing the zonal stratigraphy of a specific region of the Chalk coastline. These papers remain useful to the present day. According to Gale and Cleevely (1989), Rowe "presented zonal stratigraphy with a forceful authority which determined the course of study on the chalk of England for the next 60 years, and is best known for his work on the evolution of the Late Cretaceous irregular echinoid - *Micraster* (1899) - an important zone fossil". Rowe denigrated the use of lithology in correlation of the Chalk sections and did not believe in the worth of publishing detailed lithological sections. For many decades, therefore, he determined the approach to stratigraphy of the English Chalk. It was only with the emergence of carbonate sedimentology in the 1950's and 1960's that it was once more treated as a sediment. Rowe believed that the Chalk had been formed in deep water (1908, p. 325), stating "it is only in a deep sea deposit like the chalk, with slow, placid and uninterrupted sedimentation, taking place over vast periods of time, that we can reasonably hope to follow out every stage in the unbroken continuity of the evolution of genus." It should be noted here, with relevance to this current study, that Rowe planned a paper on the Chalk of Norfolk, but this was never written.

Much attention has been given to the mode of formation of the extensive Chalk deposits of Northwest Europe, but it was only recently that sedimentary and palaeontological evidence has proved the case for deposition in a shallow water setting. It was earlier thought to be a foraminiferal limestone analogous in origin to oceanic foraminiferal oozes at the present day, or a chemical precipitate. The fine grained, powdery nature of the Chalk formerly led to the conclusion that it was formed at great depths. Neaverson (1928), for example, placed the Chalk in the continental deep-sea area, based on the general aspect of the fauna. Depth was no more than 200 - 500 fathoms but " fine grained deposits such as chalk *may* be formed by chemical precipitation of calcium carbonate in quite

shallow water. Certain small objects known as "spheres" which were formerly thought of as being of an organic nature are now claimed to be of an oolitic nature.

Gignoux (1955, pp. 394-5), in an English edition of his 1950 textbook on stratigraphical geology, notes that calcareous sponges are localised in littoral deposits while siliceous sponges flourish in deeper or calmer seas, providing several examples. "In Hannover, where there are localities with very well preserved sponges, we can even attempt an estimate of the depth of the Chalk seas, using as standards the depths at which some of these same genera are living today." However, Guignot himself makes no direct statement that deposition in the Chalk Sea of Northwest Europe was either "deep" or "shallow". He states that "these are especially facies fossils, whose difficult identification makes them of little practical use in stratigraphy." It is probably, therefore, advisable to use more stratigraphically reliable groups.

The Chalk is now accepted as being a relatively shallow water, marine limestone, deposited at water depth of 100-600 metres (Bennison & Wright, 1975, Hancock, 1990). The current author would agree; the depth of water in the area of the present study was probably no more than a few hundred metres (pers. comm. Professor M. B. Hart, June 2000). Jenkyns (1986), raises the point that the coccoliths of the Upper Cretaceous Chalk are dissimilar to those of coeval oceanic and near-shore sediments. This may suggest an open marine, but not fully oceanic, environment of deposition. Coccolith sedimentation probably took place by faecal pellet aggregation with sedimentation rates of up to 15cm/10^3 years. This rate is considerably higher than for most recent and ancient pelagic sediments.

The faunas of the various zones show that the depth of the Upper Cretaceous seas was subject to variation. The absence of zones and sub-zones in some districts demonstrates that the apparently homogenous deposit was not formed continuously. Hence, the Chalk of northwestern Europe represents an apparent uniformity, hiding a complex sedimentological history.

Flints abound in the formation, often as lines of nodules, as tabular sheets and also in giant vertical, cylindrical forms known as Paramoudra (Bromley *et al.*, 1975; see also photographs 3 and 4 in volume 2 of this thesis). In East Anglia, the formation in the Norwich area appears to be rather uniform throughout its thickness, but a wide range of lithologies has been shown to be present. Such differences in lithology are thought to reflect depth changes in which the Chalk was deposited (Peake and Hancock, 1961, 2000;Hancock & Peake, 2000; Cox *et al.*,1989.) Appendix 1 details the lithology and biostratigraphy of the Trunch Borehole, in the form of the BGS stratigraphical log, in which apparent hardgrounds, nodular chalks and flint bands are clearly marked.

3) Rates of deposition. Hancock (1975) lists the thickness in metres (and thicknesses per million years) of the chalk deposits in Britain. Table 1.1. relates to deposition in North Norfolk. The Lower Maastrichtian data is incomplete. The thickness listed in the table is what is preserved, but thickness per million years is an estimate to allow for what has probably been removed by erosion.

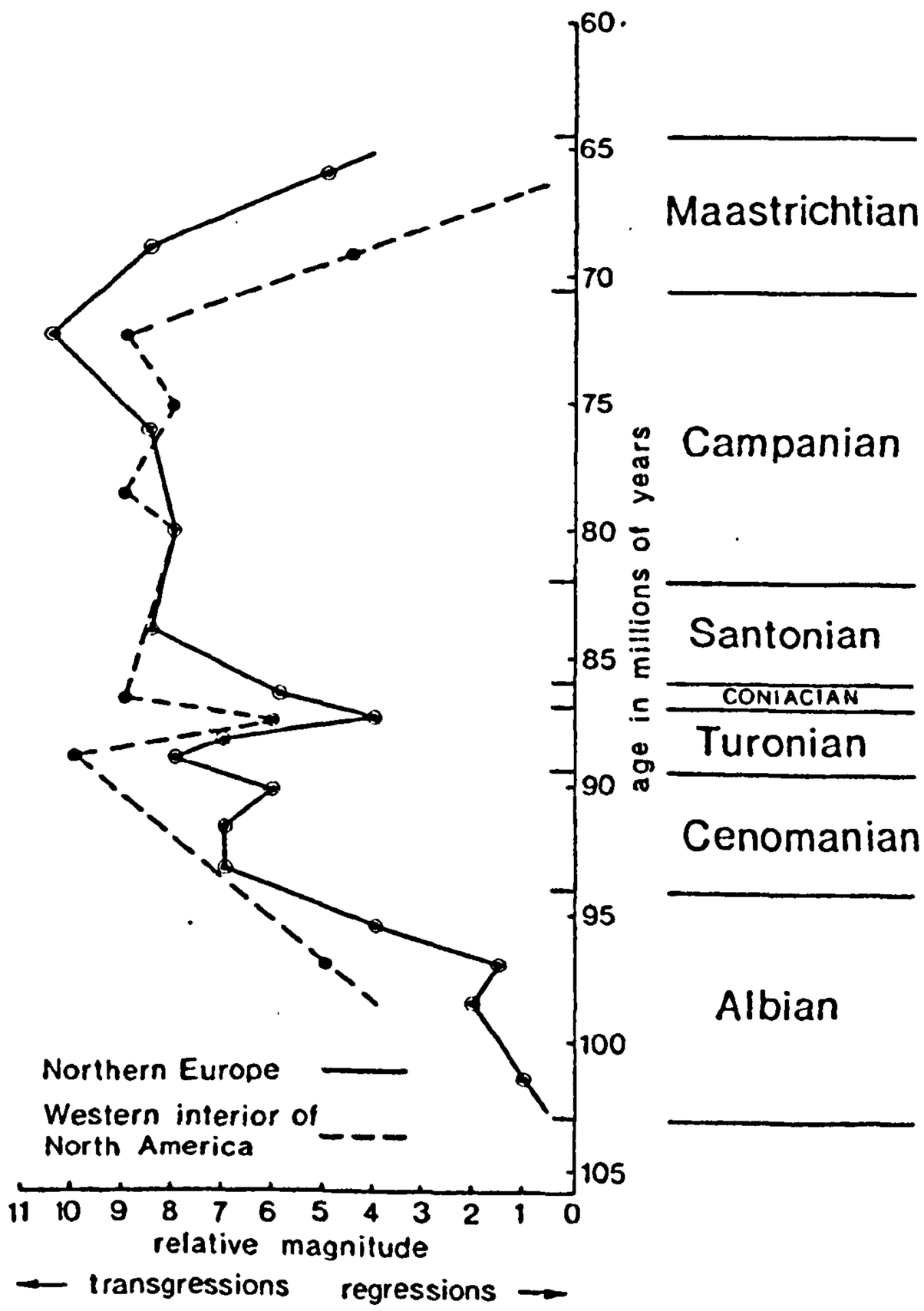
Table 1.1 : Rates of deposition in the Upper Cretaceous of Norfolk (Hancock, 1975)

stage	length of stage (Ma)	rates of deposition (and thickness) per million years	
Upper Maastrichtian			
Lower Maastrichtian	6	26.4	(14)
Upper Campanian		99.1	(17.2)
Lower Campanian	11.5	79.2	(13.8)
Santonian	4	94.5	(23.6)
Coniacian	1	22.9	(22.9)
Turonian	2.5	56.4	(22.6)
Cenomanian	4.5	16.2	(3.6)
		total = 394.7.	

Overall, the variation of depositional rates in different areas was not great, ranging from 3.6 m / million years in the Cenomanian of Norfolk to 54.3 m/million years in the Maastrichtian of the Southern North Sea (Hancock, 1975). The usual range for facies of the White Chalk is about 20-40 m/million years.

4) Sea level: Transgressive and Regressive events in the late Cretaceous:

Fig. 1.1. Trangressions of the late Cretaceous Sea in NW Europe. (adapted from Hancock, 1975)



Hancock (1975) states that the magnitude of the maximum rise must have been at least the thickness of the Chalk over stable massifs, plus the actual sea depth. As an example, there is some 400m of Chalk in Norfolk over the Brabant Massif and the Chalk Sea was probably not less than 600 metres deep. In the Upper Campanian, a rise of 600 m is indicated. It should be noted that the calculation does not allow for subsidence of the massif during the late Cretaceous.

Hays and Pitman (1973) have put forward plausible geophysical arguments in favour of late Cretaceous sea level oscillations of hundreds of metres. Corresponding oscillations in high sea levels have been plotted by Hancock, 1989, using the distribution of nodular chalks and hardgrounds in the British Chalk. Kennedy and Garrison, 1975, interpret chalk hardgrounds as the "terminal products of a sequence of deposition and early diagenetic events associated with interruptions in deposition." In 1979, Hancock and Kauffman identified 5 widespread strong transgressive peaks and Hancock can date them.

These transgressive events are as follows:

1) early late Albian peak - early part of *Callihoplites auritus* subzone
2) Early Turonian peak - early in *Collignoceras woollgari* zone,
3) Coniacian peak (relatively weak) late in stage, 1/3 way up *Inoceramus involutus* zone,
4) Middle Santonian peak - middle part of *Uintacrinus socialis* zone,
5) Campanian peak - early in *Belemnitella langei* zone.

Figure 1.2. illustrates the sea level changes in the British region (Hancock, 1990, figure 11), annotated to show the times of transgressive peaks as recognised by Hancock and Kauffman (1975).

Figure 1.2. Sea level changes during the British Upper Cretaceous

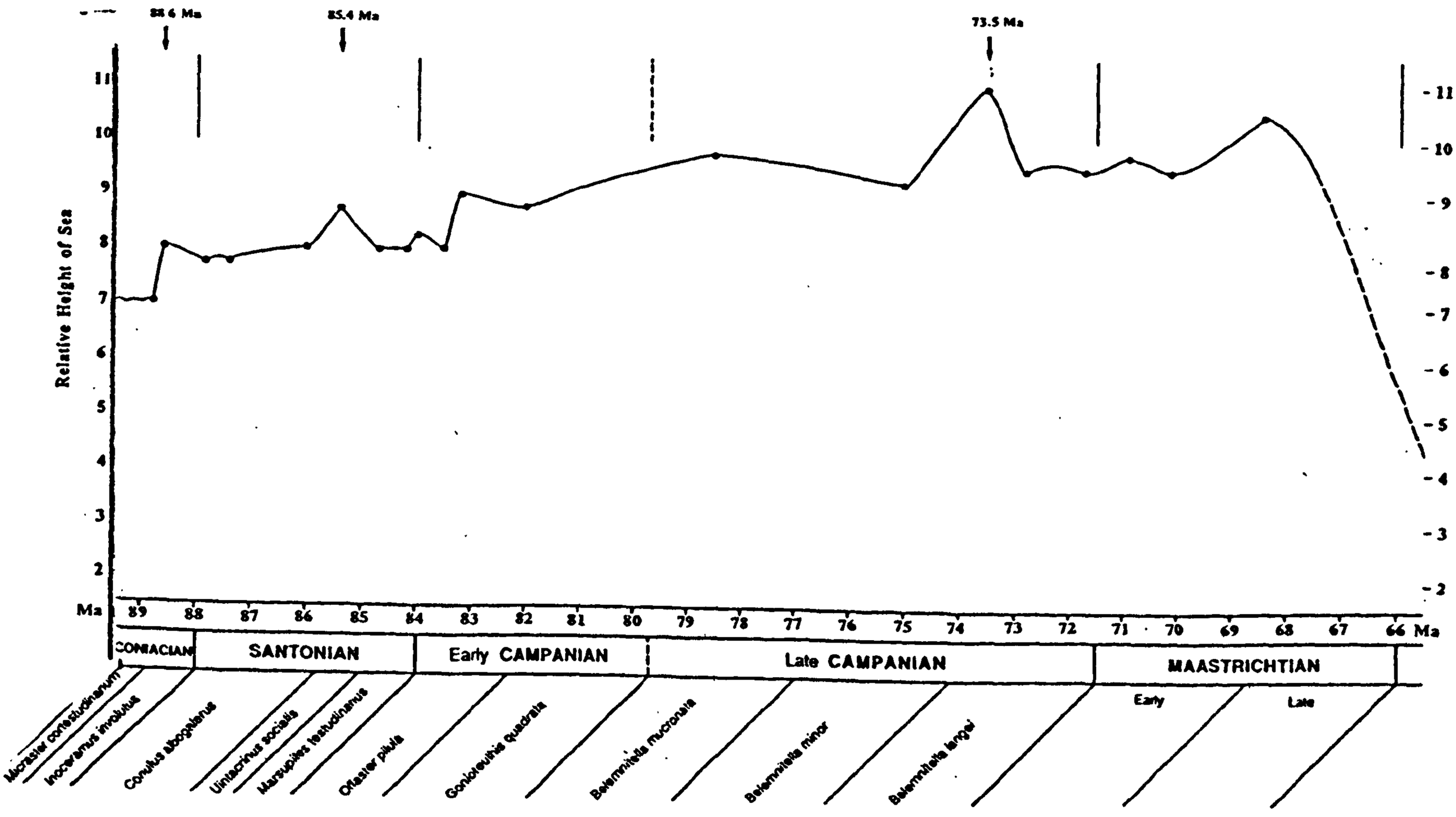
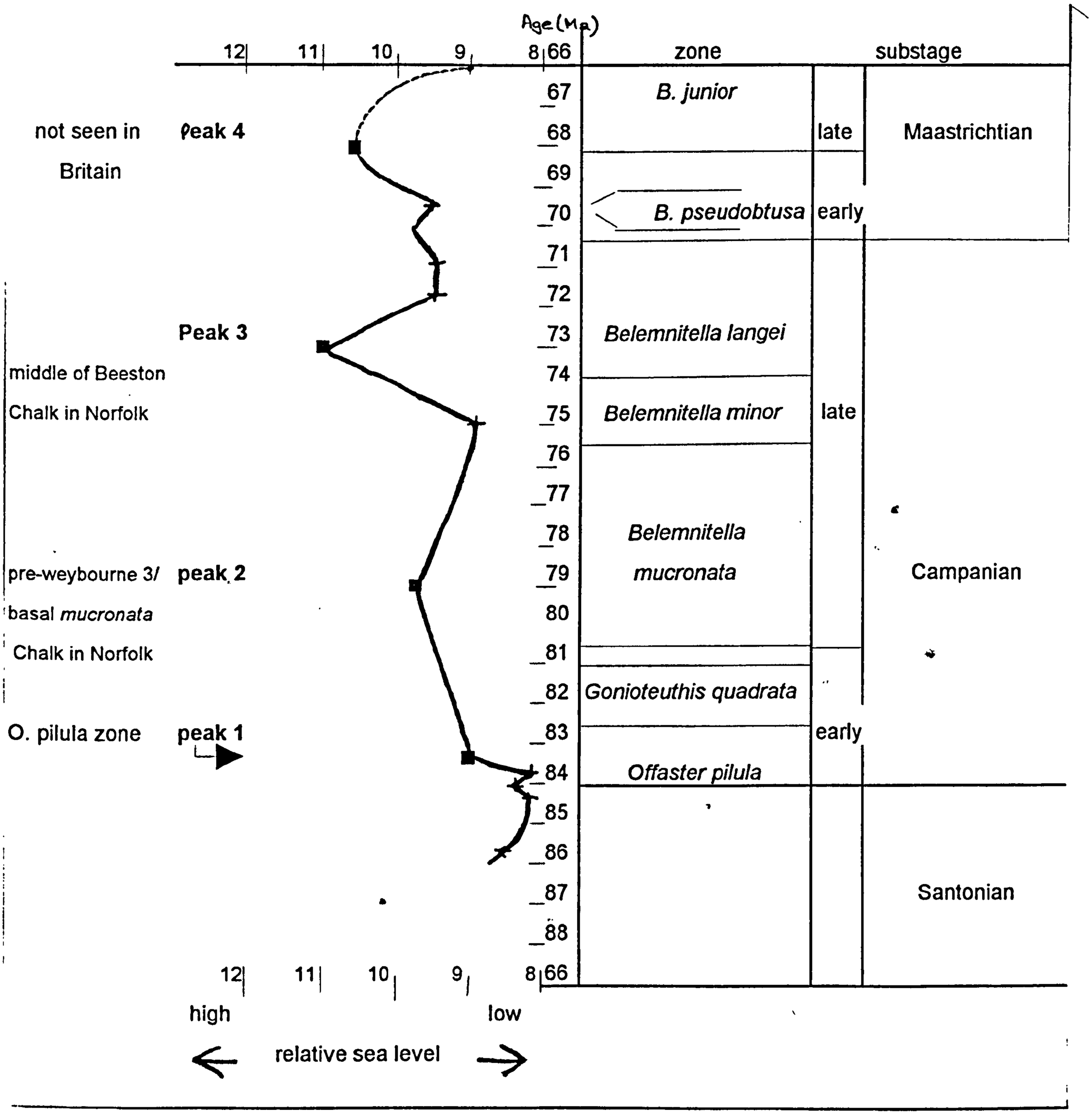


Fig. 1.3. Campanian and Maastrichtian transgressive peaks and regressive troughs in northwest Europe, adapted from Hancock, 1993 (p. 243, fig. 1) to identify the peaks as they occur in Norfolk.



Coniacian transgressive event

Coniacian Transgressive Peak (CTP) - 88.6 Ma.

Santonian transgressive event - 88-84 Ma (Hancock, 1990)

Middle Santonian Transgressive Peak (MSTP) - 85.4 Ma.

In Europe, sea levels during the Mid-Santonian were higher than at any prior time during the Cretaceous.

Campanian transgressive event - 84 - 71.5 Ma (Hancock, 1990)

Late Campanian Transgressive Peak (LCTP) - 73.5 Ma

In all regions of Britain where post-Santonian Chalk survives, the sea was "sufficiently deep for it to be difficult for nodular chalks to be developed" (Hancock, 1990). Throughout the Campanian and Maastrichtian, there is only one piece of strong direct evidence in Britain for changes in shoreline position: the great transgressive spread of the Chalk at a relatively late stage in the Late Campanian.

Maastrichtian transgressive event - 71.5 - 66 Ma.

Generally, there was a continuous widespread transgression throughout much of the period marked by chalk deposition. Water depth gradually increased until the interval represented by the *Micraster coranguinum* biozone. In the Trunch Borehole, this corresponds to the Middle Coniacian to mid-Santonian. In higher zones, the proportional elevation of echinoid tests decreases. This is taken to indicate shallowing of the water, supported by the increased importance of gastropods in the *Belemnitella mucronata* zone, which in the Trunch Borehole corresponds to the Upper Campanian Paramoudra Chalk, Beeston Chalk, Catton sponge Beds, Weybourne Chalk and basal *mucronata* Chalk. Reference should be made to appendix 1 - the BGS biostratigraphical log for this borehole.

Hancock (1993) has produced a transatlantic correlation in the Campanian and Maastrichtian stages by eustatic sea level changes. In this, he states that "by using nodular chalks and hardgrounds to date regressive troughs and the mid-point between pairs of these to date transgressive peaks, it has been possible to elucidate a more accurate pattern of sea level changes through the Late Cretaceous in north-west Europe." This is reproduced in figure 1.3.

The principle peaks in Europe (detailed earlier in the 1990 publication and summarised above in this thesis) are all, with the exception of the Late Maastrichtian peak, identifiable in the USA.

Four main transgressive peaks are identified from the Campanian to Maastrichtian in northwest Europe, of which three also occur in Norfolk. Figure 1.3. illustrates the position of these peaks. The present author has annotated the original (1993, p. 243, figure 1) to provide further information about the subdivisions and/or zones in which they occur:

Peak 1 - "subzone of *Echinocorys truncata* in the zone of *Offaster pilula* of the Chalk in southern England.", interpreted as the *O. pilula* Zone of the Norfolk Chalk.

Peak 2 - This peak is difficult to date due to the large distance between the two defining troughs. The lower trough is at the base of the *Gonioteuthis quadrata* Zone, as it is used in England (*sensu anglico*) (Peake & Hancock, 1970, p. 339c; Christensen, 1991; Hancock, 1993, p.243). In Germany, this zone extends much lower than the base of the *quadrata* Zone. The upper trough is

represented by the Catton Sponge Beds in Norfolk. This places Peak 2 in the basal *B. mucronata* Zone Chalk, as it is defined in the UK. In Norfolk, this equates to the pre-Weybourne 3 of Wood (1988). Peak 3 is prominent and well defined in the lithostratigraphy, placed in the Beeston Chalk of Norfolk.

However, when the ostracod evidence from the present study is examined, especially in terms of the % of platycopids, it becomes clear that Hancock's positioning of transgressive peaks and regressive troughs based on hardgrounds is rather oversimplified. This is discussed further in chapter 4 of this thesis and Whatley, Pyne and Wilkinson (in press).

Nodular beds represent periods of shallower water deposition, while marls (e. g. the Wells Marl in the Trunch Borehole) represent an increase in the input of terrigenous material. Such an increase might be due to an elevation of a neighbouring land area with consequent increased processes of erosion.

Challinor (1959, reprinted 1970, p. 75) states that the "conditions under which the Chalk was formed was apparently uniform over wide areas; moreover deposition appears to have been almost continuous. No appreciable gaps comparable with the frequent non-sequences in Jurassic strata have been detected, though the possibility of their occurrence cannot be denied. Consequently, the succession of beds, though subject to local variations in lithology and other characters, is fairly regular over wide areas, and the fossils reveal a true and almost unbroken succession of faunas. Indeed, no other formation, except perhaps the graptolitic facies of the Ordovician and Silurian, provides a more complete record of evolution in slowly changing organisms." The assumption that deposition appears to have been almost constant with no appreciable gaps does not take into account the presence of nodular chalks and hardgrounds. These are products of diagenetic cementation just beneath the sea floor, generally associated with reduced sedimentation rates or hiatuses (proven breaks in deposition). Many authors (e.g. Bromley, 1967, 1975; Kennedy & Garrison, 1975; Hancock, 1990; Gale, 1996; Robasynski *et al.,* 1998; Grant *et al.,* 1999) have extensively detailed Upper Cretaceous hardgrounds and nodular chalks made up of discrete carbonate concretions with diffuse boundaries, separated by soft burrowfill Chalk. Encroaching lithification progressively reduces the burrow diameter, producing a "lithified chalk framework" (Kennedy & Garrison, 1975; Bromley, 1975; Gale, 1996, p. 184). Sea floor exposure of the lithified chalk results in the formation of a true hardground, which can be identified by the presence of boring and encrusting organisms and the replacement or coating of the surface by such minerals as glauconite or phosphate.

Trace fossils and their relevance to palaeodepth interpretation

In the BGS stratigraphical log for the Trunch borehole (Appendix 1), several types of trace fossil are seen. These include *Zoophycos, Chondrites* and thallassinoid burrows as well as bendekreide and other unspecified burrowtypes. Trace fossils provide an unequivocal *in situ* record of animal activities in or on the substrate surface (Frey & Seilacher, 1980; Johnson & Baldwin, 1986). This is especially important in palaeoenvironmental analysis, because each trace provides a partial record of both individual organism activity and substrate conditions.

Figure 1.4. A generalised bathymetrical distribution of trace fossil communities

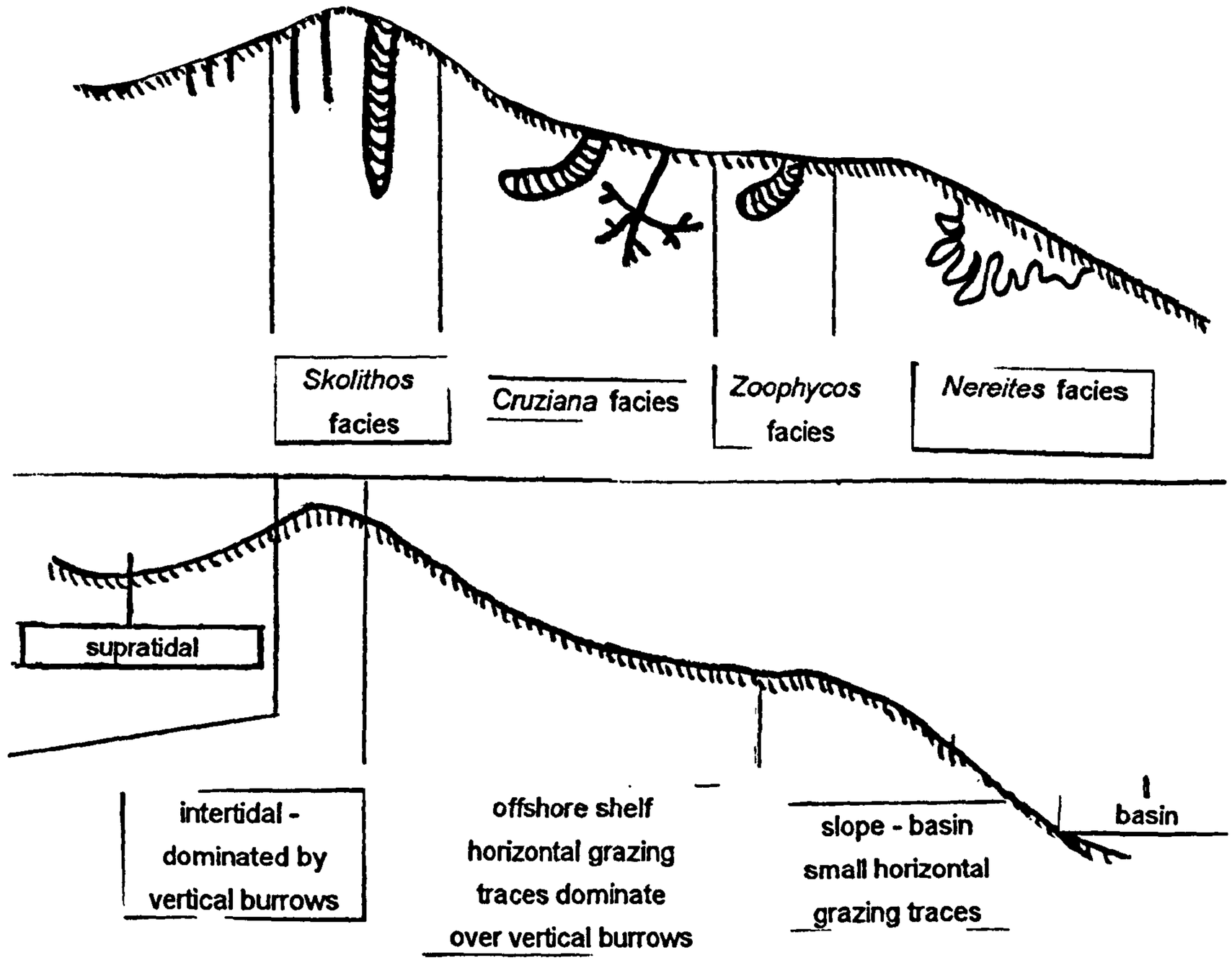
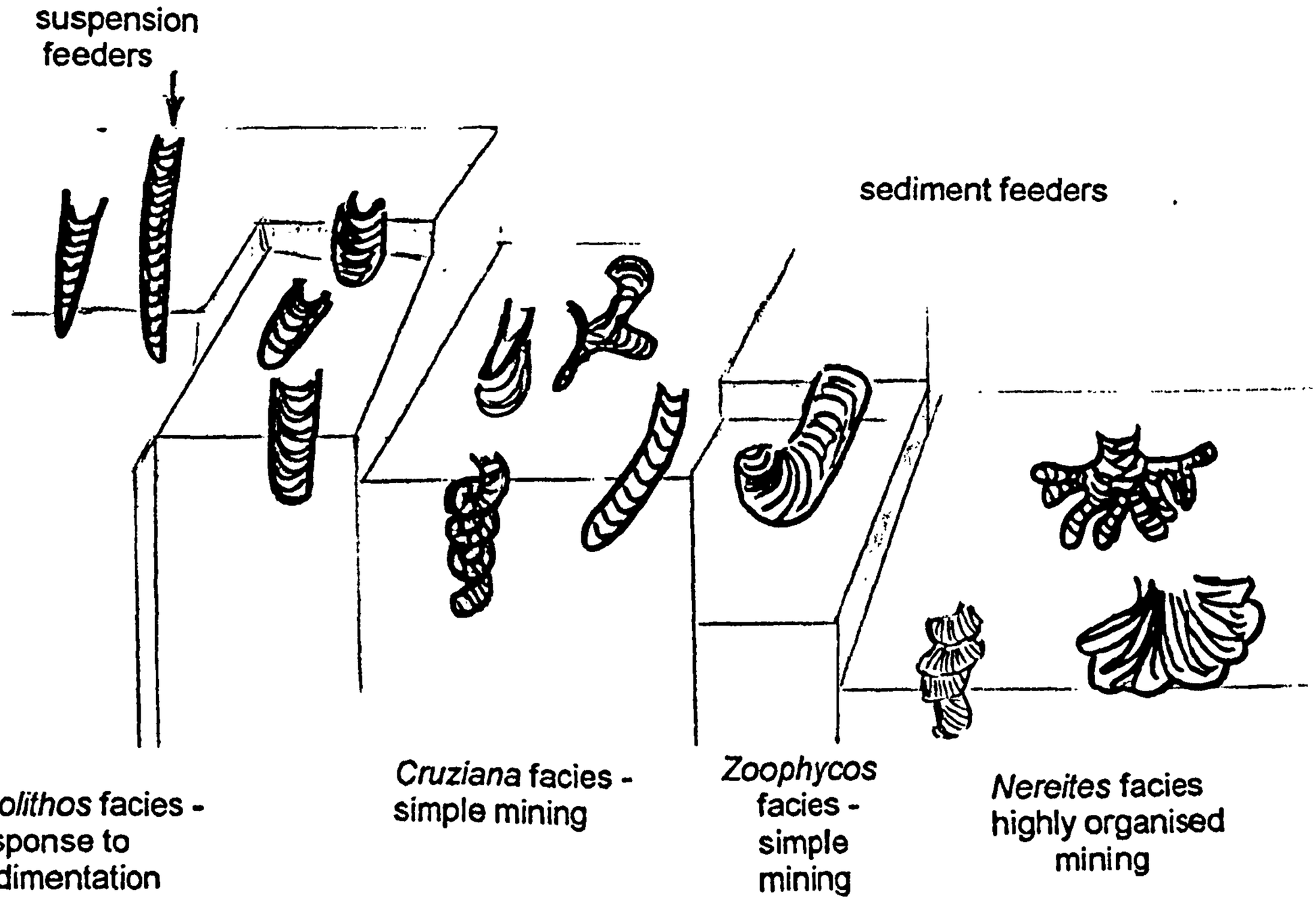


Figure 1.5. Trace fossil facies and biogenic activity (adapted from Johnson & Baldwin, fig. 9.31C).



Trace fossils characterising the shelf environment mainly record the activities of suspension feeders.

In deeper water or low energy environments, the proportion of elaborate sediment feeders generally increases. This forms the basis of Seilacher's 1967 bathymetrical zonation of trace fossil communities (Johnson & Baldwin, 1986, p. 256, fig. 9.31, reproduced in this thesis as fig. 1.5).

It should be noted, however, that since the shelf environment is subjected to a wide range of physical energy levels and diverse substrate types, there are probably several different types of trace fossil community. Seilacher's model should be treated as a guide to approximate palaeoenvironments, taking into account the effects of localised conditions on the communities under consideration. Based on the abundance of *Zoophycos* type traces, most of the Trunch Borehole assemblages detailed in this study could be placed on the middle to outer shelf, in conditions of normal salinity and relatively low levels of current activity, where horizontal traces tend to dominate over vertical burrows. *Thalassinoides* is, according to Seilacher, present in the *Cruziana* association occurring on the shallow to intermediate shelf, while *Chondrites* is found in more than one assemblage.

The Cretaceous geology, lithology and biostratigraphy of East Anglia - a summary.

In the area of East Anglia, the Lower Cretaceous Gault, Greensand and red-rocks (Kennedy, 1969, 1970; Drummond, 1970, Wilkinson, 1988a MS; see also this thesis for an overview of the Lower Cretaceous), are overlain by a more uniform formation - the Chalk. This change in sedimentation followed a gradual sinking of the sea floor across the whole area that is now the British Isles, continuing until a great thickness of calcareous ooze had accumulated. Processes of consolidation formed the Chalk, which in Norfolk attains a maximum thickness of 1400 feet (c. 430 metres). The western boundary of the Chalk can be traced from the escarpment in Bedford to the North-East of Cambridge (See Chatwin, 1961), turning North to Hunstanton, where it then extends eastwards, dipping at a slight angle towards the east.

The Upper Chalk in Norfolk is thicker than elsewhere in Britain. The bulk of the material is a relatively pure rock which is white or creamy in colour. Flint is relatively common, formed after the initial calcareous ooze was deposited by the separation of the contained silica. Fossils are common and highly diverse and the species numerous, with each zonal division having a distinctive assemblage. Several zonal schemes exist, which are detailed earlier in chapter 1 of this thesis, but most of the zone fossils employed are the same. In the lower zones, the echinoid *Micraster (Micraster coranguinum)* is a distinctive component. Higher up, detached plates of the crinoid *Marsupites (M. testudinarius)* marks definite horizons of limited vertical range. The remainder of the Chalk is divided into three belemnite zones. Firstly, *Gonioteuthis quadrata,* underlying a zone which is characterised by *Belemnitella mucronata.* The highest belemnite zone (zone 3) is marked by the presence of *Belemnitella lanceolata*. Echinoids of the genus *Echinocorys (e.g. E. scutata)* range throughout the upper chalk and the eponymous species exhibits shape variations which generally correspond to horizons.

Offaster pilula has been recorded from the belemnite zones. Lamellibranch shells are common with genera such as *Ostrea, Pecten* and *Spondylus* being well represented. *Inoceramus* is

the most common and is of some zonal value, since several species are typical of different horizons. Brachiopods are also common; the more usual forms being rhynchonellid and terabratulinids (e.g. *Cretirhynchia* and *Carneithyris*).

Christensen (1988), surveys the "current status of our knowledge of the Upper Cretaceous belemnites of Europe. The late Cretaceous North Temperate Realm, including the North American and Northern European Provinces are characterised by the Belemnitellidae." The same author (1991) details belemnites from the Coniacian - Lower Campanian Chalk of Norfolk and Southern England. The following genera are present in East Anglia during the interval of the current study:

Belemnitella D'Orbigny *B. langei, B. senior, B. mucronata* - the zone fossil of the Upper Campanian), *B. lanceolata* - zone fossil of Lower Maastrichtian sponge Beds of Sidestrand in the Trunch Borehole.

Belemnella Nowak

Gonioteuthis Bayle *G. quadrata* - zone fossil of the Lower Campanian in the Trunch Borehole and outcrop samples.

Christensen (1995) studied in the genus *Belemnella* from the Upper Campanian and Lower Maastrichtian Chalk of Norfolk.

Robaszynski *et al.* (1985), writing on the Campanian-Maastrichtian boundary in the Chalky facies close to the type Maastrichtian area, state that "biostratigraphical evidence is given with the distribution of macrofossils, especially belemnites and other cephalopods and of microfossils such as benthic and planktonic foraminifera, nannoplankton and dinoflagellates. Palaeoenvironmental characteristics are suggested after quantitative study on fossil groups giving good palaeoecological information, such as mesofossils, ostracoda, spores and pollen. Thus, from one or another fossil group, biostratigraphical zones and ecozones are defined." The Zeven Vegen member is considered to be Upper Campanian in age; the Beutanaken Member with *B. lanceolata inflata* is lower Lower Maastrichtian. This zonation correlates to the zone fossils used in the Trunch Borehole and this relationship can be summarised as follows:

<table>
<tr><td>Robaszynski et al., 1985
Zeven Vegen Member</td><td>this study, Trunch Borehole
Paramoudra Chalk
Beeston Chalk
Catton Sponge Beds
Weybourne Chalk
basal mucronata Chalk</td></tr>
<tr><td>Belemnitella mucronata
Upper Campanian</td><td>Belemnitella mucronata
Upper Campanian</td></tr>
<tr><td>Beutnaken Member
Belemnitella lancolata inflata
lower Lower Maastrichtian</td><td>Sidestrand Chalk
Belemnitella lanceolata
Lower Maastrichtian</td></tr>
</table>

Johansen & Surlyk's (1990) work on brachiopods and the stratigraphy of the Upper Campanian and Lower Maastrichtian Chalk of Norfolk is useful. The various zones and subdivisions used in the present study are described in more detail (1990, pp 824-831).

When used in conjunction with such recent publications as Christensen, 1991, 1995; Peake & Hancock, 2000 and Hancock and Peake, 2000, the present author found it possible to relate macrofossil biostratigraphy to lithostratigraphy with a high degree of certainty. The biostratigraphy of the Trunch Borehole was detailed in the BGS log, included in this thesis for reference as Appendix 1, and also in Burnett, 1988 MS., McArthur *et al.*, 1984, Wood *et al.*, 1994.

British Cretaceous Ostracoda taxonomy.

Our knowledge of British Cretaceous Ostracoda is somewhat incomplete but in general, the Lower Cretaceous has been studied in more detail than the Upper Cretaceous. The bulk of early work was on Albian and early Cretaceous ostracods. Recent years have seen a "generic explosion" producing a number of synonyms. In many cases, the criteria for generic assignment of species are tenuous. Due to the long history of research in both Europe and North America, this has inevitably resulted in a large number of species with many problems of taxonomy, synonymy and interpretation. The clearest example of this is the large number of forms originally assigned to *Cythereis*, despite a wide variety of shapes, ornament and hinge structure. In 1948, Sylvester-Bradley restricted the use of *Cythereis* to the Cretaceous and accommodated only those species with a paramphidont hinge. The genus is discussed in more detail in chapter 2 of this thesis. The genus *Cytheropteron* has also been similarly confused and is also dealt with in this chapter.

Ager, writing in 1963, states that "the overwhelming bias of Palaeontology in Geology has been towards the elucidation of Stratigraphy, but it is becoming increasingly apparent that the great part of stratigraphical palaeontology is meaningless without sufficient consideration of palaeontological factors." A good example is the Shenley Limestone of Bedfordshire. This unit appeared to be Cenomanian on initial examination, based on the presence of highly fossiliferous limestone lenticles, which were found above and below Albian clays. The fauna, however, appeared to match Cenomanian faunas of surrounding areas. Eventually, this hypothesis was rejected. The Shenley Limestone has been proved to be Lower Albian in age (Ager, 1963) and the Cenomanian aspect of the fauna is nothing more than a "coincidence of facies."

Upper Cretaceous faunal evolution and morphological trends.

The inception of the Chalk Sea coincided largely with the transition from older to younger faunas. Trachlyleberid genera develop greatly and a number of genera dominant in the Lower Cretaceous disappear (Neale, 1978; Van Morkhoven, 1962, 1963, 1986). Neale also states that Cretaceous faunal evolution generally exhibits trends that are closely linked with the increasing extension of the areas affected by marine influence.

New genera appearing in the Chalk include:

Alatacythere, Pterygocythere, Pterygocythereis, Trachyleberidea

This corresponds with the disappearance of such genera as:

Dolocytheridea, Paranotacythere,

Protocythere - split into three genera *Protocythere* Triebel, 1938, *Mandocythere* Grundel, 1964 and *Costacythere* Grundel, 1966. Damotte (1968) describes the three from the Cretaceous Paris Basin and compares and contrasts each genus (1968, table 1, p. 385; see also Wilkinson, 1988a, MS).

In the Cretaceous, genera more typical of the Cainozoic (e.g. *Paracyprideis, Pterygocythereis, Krithe, Argilloecia* and *Xestoleberis)* appear progressively. *Bairdia (sensu lato* - according to Maddocks, 1969, *Bairdia (*sensu stricto) is to be reserved for Palaeozoic members and all post-Palaeozoic species should be classified as *Bairdoppilata), Bairdoppilata* and *Cytherella* are common. In the Senonian, the genera *Brachycythere, Haplocytheridea* and *Phacorhabdotus* appear together with the last species of *Cythereis (sensu stricto),* as well as the first representatives of the Cytherettinae (e.g. *Paracytheretta* and *Buntonia)* and the first Hemicytherinae (cf. *Quadracythere*).

Several authors (e.g. Weaver, 1982; Neale, 1982) conclude that very low oxygen content in the bottom waters was the cause of reduced ostracod faunal diversity. Although this cannot be proved with absolute certainty, it is probably correct. Ratios of podocopid and platycopid ostracods could be used to identify such intervals of reduced oxygenation.

Weaver (1982, p. 100), commenting on the stratigraphical distribution of ostracoda during the Cenomanian in Southern England, notes marked faunal changes. Changes were "not only at the species level; many genera also disappeared e.g. *Dolocytheridea, Mandocythere, Platycythereis, Protocythere* and *Schuleridea.* Several new genera appear during the Cenomanian e.g. *Amphicytherura, Curfsina, Idiocythere, Oertliella, Trachyleberis* and *Xestoleberis.* These genera have all been recorded from Upper Cretaceous deposits, four out of six of these appear in the Coniacian to Lower Maastrichtian material of the present study, and the last three also have recent representatives. Weaver also notes that "as in most Cretaceous sequences, the Trachyleberididae are the most important group; they are common, they evolved rapidly and are strong enough to withstand processing." In the material of the present study (Trunch Borehole assemblages), in samples containing normal marine assemblages genera belonging to the Trachyleberididae are dominant. In samples where the oxygen levels were reduced (kenoxic rather than anoxic), filter feeding platycopids belonging to the genera *Cytherella* and *Cytherelloidea* replace trachyleberids as the dominant component.

Whatley and Stephens (1976) in a study of faunal evolution during the late Cretaceous note that the highest level of evolutionary activity among the Mesozoic Cytheracea took place during the Senonian and Maastrichtian (Whatley, 1986, 1988 and Whatley & Ballent, 1996). In terms of the total number of species per stage, there is an irregular increase during the Triassic and Jurassic. Between the Turonian and Senonian stages, the increment in the total number of species is almost 100% of the

total fauna and a further large increment takes place up into the Maastrichtian. This is shown in table 1.2a, adapted from Whatley & Stephens, 1976.

Table 1.2 a– Faunal evolution during the Cretaceous; total number of species present:

	total number of species	increment
Upper Cretaceous	1581	
		581
Lower Cretaceous	1000	
Upper Jurassic	1111	

In terms of new species, the Cretaceous makes up 59.93% of the total for the Mesozoic. With respect to new genera, this total is 47.11%.

Table 1.2b- Number of species and genera per stage and species and genera per division:

substage	species/stage	species/division	genera/stage	genera/division
Maastrichtian	611		88	
Senonian	467		81	
		1581		252
Turonian	244		28	
Cenomanian	259		55	

Table 1.2c Number of families per stage

Maastrichtian	18
Senonian	18
Turonian	18
Cenomanian	14

Whatley (1988, p. 1037), examining patterns and rates of evolution among Mesozoic ostracoda, notes that the large scale diversity increase in total ostracod species in the Aptian to Maastrichtian interval is principally due to Cytheracea, but Bairdiacea and Platycopina also figure. This interval was one of "protracted and almost uninterrupted transgression which culminated in the Upper Cretaceous in one of the highest sea level rises of the Phanerozoic." The increase in diversity is, with the exception of the Turonian (a time when origination and extinction were extremely low for the Upper Cretaceous), regular and represents the only time in the Mesozoic when it is possible to correlate a transgressive event with increased diversity. During the Albian-Maastrichtian, evolutionary events within the Cytheracea are of major significance. The amphidont hinge, a structure which first appeared in the Oxfordian, does not appear to have been successful in the Jurassic but from the marine Cretaceous, especially from the Aptian onwards, this hinge type is increasingly common. The interval also saw a hinge type evolution from the hemi-amphidont to the more advanced holamphidont. The consequent adaptive radiation of the Trachyleberididae and Brachycytheridea is related to high diversity levels in the Senonian and Maastrichtian.

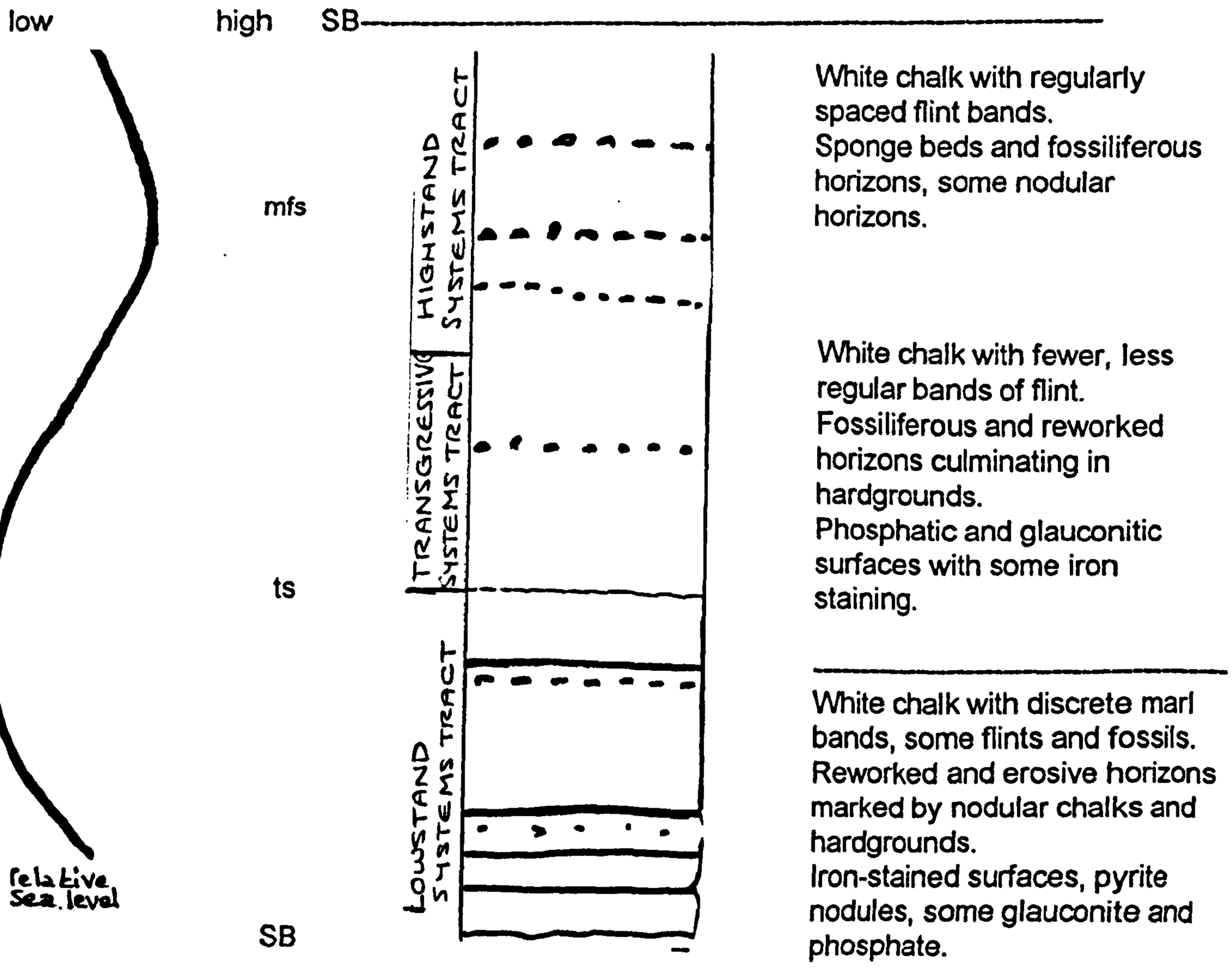
Cretaceous Sequence Stratigraphy

The concept of sequence stratigraphy has been developed over the last decade or so from existing stratigraphical methods. It has been used by Robaszynski *et al.*, 1998 (p. 363), in the Anglo-Paris Basin, exemplified by the Cenomanian. In this stage, biostratigraphical resolution is very high. Gale *et al.*, 1999, write that it "affords one of the best opportunities for the development of ultra-high stage resolution stratigraphy in the Mesozoic." This is, in part, because it "contains an ammonite fauna of widespread distribution which enables correlation with a resolution of 0.3 Ma, and displays the basis for an orbitally tuned timescale." Juignet & Breton (1992) and Hart *et al.*, 1992, have produced detailed stratigraphies for the mid-Cretaceous of the Western Paris Basin and Southern England. Gale (1996) presented a Turonian correlation and stratigraphy for the Chalk of Southern England, using lithostratigraphical marker beds and biostratigraphy. Gräfe, 1999, documents foraminiferal evidence for Cenomanian sequence stratigraphy and palaeoceanography in a middle to Upper Cenomanian Chalk succession in the northwestern Paris Basin (also Paul *et al.*, 1999).

Gale *et al.*, 1999, worked on the Coniacian succession of the Anglo-Paris basin. According to this study, the Upper Cretaceous Chalk of Northern Europe was "deposited in an open, epi-continental sea, during a period of high global eustatic sea level...a unique depositional setting requiring modification of the sequence stratigraphical approach." The authors provide a framework for analysis of Upper Cretaceous Chalks using such methods and define "an ideal chalk sequence" (p. 19) to allow sequence stratigraphical analysis of chalk with flint successions - reproduced in fig. 1.6.

Using this model, the Santonian to Lower Maastrichtian horizons of the Trunch Borehole could be correlated and a sequence stratigraphical section produced, following on from the Coniacian interval published by Grant *et al.*, 1999 (p. 25, fig. 8). This was beyond the scope of this present work.

Figure 1.6. An idealised Chalk sequence (after Grant et al., 1999, fig. 1)



Neaverson (1928) divides the English Upper Chalk into 7 subdivisions, as shown in table 1.3 below. Comparison with the continental Senonian shows that the British succession is "Incomplete with the uppermost portion being removed by the denudation before deposition of overlying Tertiary rocks."

Table 1.3. Subdivision of the English Upper Chalk (adapted from Neaverson, 1928) .

Zone	biozone	notes
1	*Holaster planus* zone	Fauna has a wide distribution in Southern and central England, and has been traced as far as Norfolk. Presence of numerous cephalopods (e.g. *Scaphites)* gastropods abundant, common lamellibranch (e.g. *Spondylus*, *Inoceramus),* sponges and simple corals.
2	*Micraster cor-testudinarium*	soft, white blocky chalk with veins of tabular flint, regular courses of flint nodules. Associated fossils such as *Inoceramus involutus.*
3	*Micraster coranguinum*	
4	*Echinocorys scutatus*	
5	*Marsupites testudinarius*	generally soft, powdery chalk. free swimming crinoids (e.g. *Uintacrinus westfalicus, Uintacrinus socialis.*
6	*Actinocamax quadratus/ Offaster pilula* zone	
7	*Belemnitella mucronata*	soft white chalk, numerous flints "Paramoudras connections" - a feature of this zone in Norfolk -see Trunch Borehole Log.

Table 1.4. Zones of the British Chalk, adapted from Bennison and Wright (1975), pg. 329, table 14.6.

Maastrichtian	*Liostrata lunata*
	Belemnitella mucronata
Campanian	*Gonioteuthis quadrata*
	Offaster pilula
	Marsupites testudinarium
Santonian	*Uintacrinus socialis*
	Micraster coranguinum
	Micraster cor-testudinarius
Coniacian	*Holoaster planus*
	Terabratulina lata
Turonian	*Orbirhynchia cuvieri*
	Inoceramus lamarki

Table 1.5. Divisions of the Senonian stage in the East Midlands according to Keen, 1968.

Stage	Zone	Zonal subdivision
SENONIAN	*Belemnitella mucronata* *Actinocamax quadratus* *Offaster pilula*	*Offaster pilula*
		Echinocorys scutata var. *depressula*
		Marsupites testudinarius
	Marsupites testudinarius	
		Uintacrinus westfalicus
	Micraster coranguinum	
	Micraster cortestudinarium	

Table 1.6. Stratigraphical Terminology of the exposed Upper Chalk in the Norwich district : adapted from Cox et al., 1989, table 2, pg. 12.

stage	zone	Peake and Hancock 1961 subdivisions	Provisional faunal belts (Wood 1988.)
MA			*Belemnella lanceolata*
		Paramoudra Chalk	Paramoudra 2 Paramoudra 1
		Beeston Chalk	Beeston Chalk
		Catton Sponge Bed	Catton Sponge Bed
-	CA		
		Weybourne Chalk	Weybourne 3
			Weybourne 2
			Weybourne 1
Belemnitella mucronata		Eaton Chalk	Pre-Weybourne 5 Pre-Weybourne 4
basal Mucronata zone			Pre-Weybourne 3 Pre-Weybourne 2 Pre-Weybourne 1
Gonioteuthis zone			

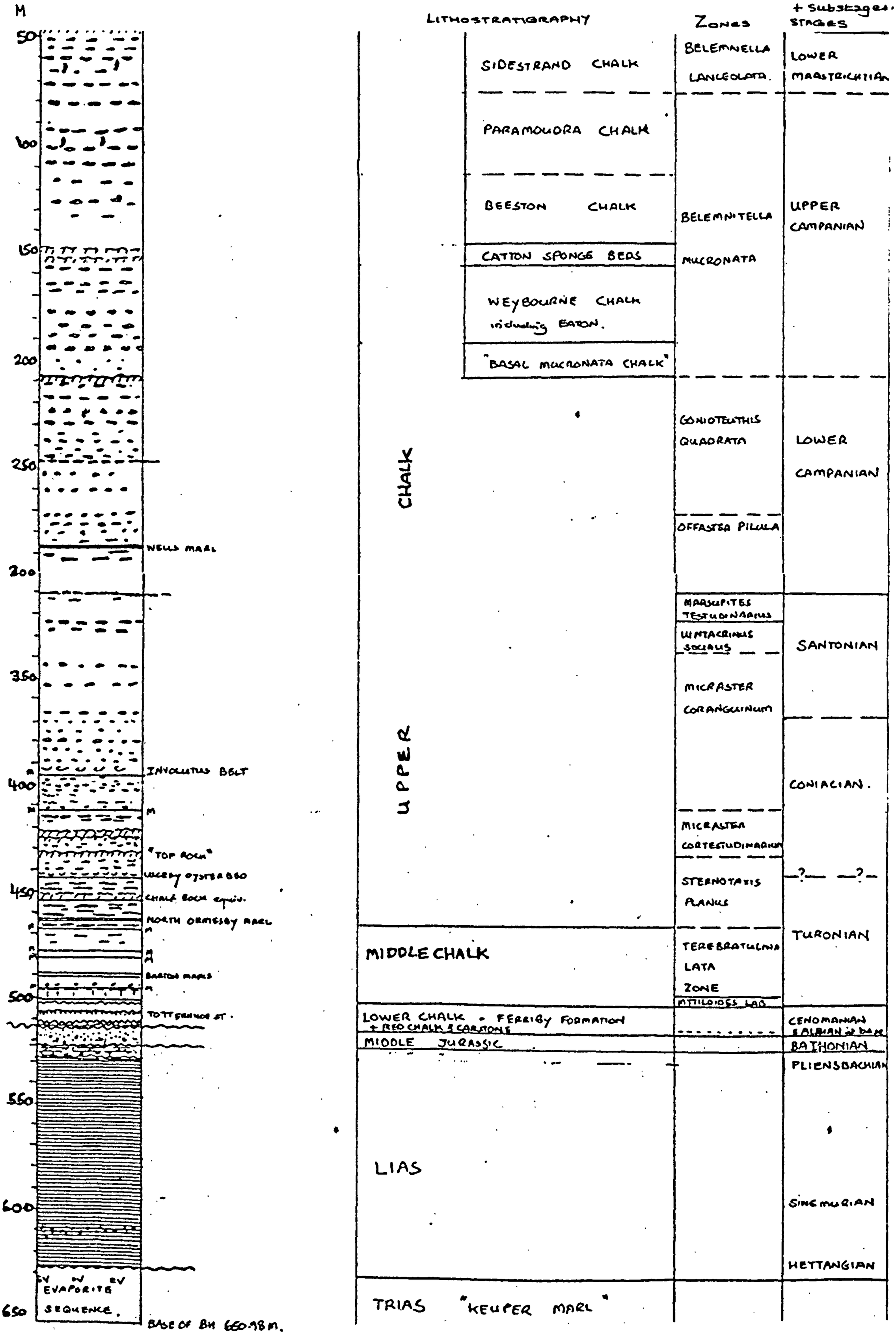
There are two points to be made regarding figure 1.6, arising from the work of other authors.

*1 - Hancock and Peake, 2000 (p. 31, fig.3, originally from Christensen, 1995) divide the Lower Maastrichtian into two "traditional belemnite zones"; *Belemnella lanceolata* comprising the pre-*Porosphaera, Porosphaera* Beds and Trimingham Sponge Beds, and *Belemnella occidentalis* comprising the *O. lunata* Chalk and Grey Beds. For the purposes of this thesis, *B. lanceolata* is used for all Lower Maastrichtian samples to conform with the BGS stratigraphical logs (Appendix 1). Reference should also be made to Johansen & Surlyk, 1990, pp. 824-830, fig. 9.

Burnett (1988, MS, p. 32) notes that the "apportioning of the top Cretaceous sediments in the Trunch Borehole to the *lanceolata* Zone by Gallois & Morter (1975) was found, on nannofossil evidence, to be unjustified." In explanation, she states that "this part of the borehole is, in fact, of latest Campanian (mucronata Zone) age and that, therefore, the Trunch Borehole does not penetrate the Maastrichtian

*2 - The BGS log (Appendix 1) and Cox *et al.*; 1989, McArthur *et al.*, 1994, Wood *et al.*, 1994, all use *B. mucronata* for the entire Upper Campanian substage. Hancock, 1990, 1993; Hancock & Peake, 2000; Peake & Hancock, 2000, and Christensen, 1991, divide the substage into three parts defined by *B. mucronata*, *B. minor* and *B. langei.* The present author retains *B. mucronata* throughout to conform to the BGS stratigraphical and lithological logs and past work in Norfolk.

Fig. 1.7. Outline stratigraphy of the Trunch Borehole (A. A. Morter, 10/4/84)



TRUNCH BOREHOLE - SUMMARY OF THE DOWNCORE LITHOLOGY AND BIOSTRATIGRAPHY

Location: Trunch, near Mundesley, Norfolk, IGS Trunch, 6 inch: 10 000 map reference - TG 23 SE; grid reference. TG 29330.34550.

Borehole sunk by Foraky Ltd. , September 1974-1975.

Prepared samples loaned to the present author BGS loan number 97/33).

All information about the samples is taken from the Institute of Geological Sciences BGS record of borehole, 91 page log; see appendix 1 for summary diagram of lithology and biostratigraphy.

Lower Maastrichtian *Belemnella lanceolata* Zone, SAG 213-231

SAG 231, 221 and 217 = the pre-*Porosphaera* Beds of Peake & Hancock (1961, 1970, 2000; Hancock & Peake, 2000). SAG 216, 213 = *Porosphaera* Beds. The Lower Maastrichtian samples appear inn figure 1.8a, annotated from the original BGS logs.

Chalk greyish with marly streaks and bendekreide; moderately fossiliferous with fish debris, belemnite fragments, calcitic shells. Flints large with black, slightly carinous cantre and thin, light-grey cortex. 2 possible flint bands; 1 at 41.17, other at 47.50m. At 60.10m, the chalk is soft, greyish white, slightly marly with grey marly burrowfills, bendekreide; *Neithea* with fish bed and *Austinocrinus,* becoming more marly below 60.80m, soft marly chalk (SAG 221).

Upper Campanian Belemnitella mucronata Zone, Paramoudra Chalk, SAG 241-307, 62.53-122.20m depth.

Chalk white, slightly marly with grey marl streaks and bendekreide. Many small burrows, calcite worm tubes, terabratulinoid fragments and ostreid oysters?, thalassinoid flints. Attached fossils at 64.31m, belemnite and echinoderm fragments downcore, flints very large (140mm length, 80mm wide), dark, semi-translucent, coffee brown with rare, small, grisly inclusion; thin chalky cortex, carious, numerous burrowfills of a grey-white marly chalk. These grade into a similar material showing complex burrow structures, picked out by various shades of pale grey marly chalk with numerous short, vertical joints. Calcitic fossils relatively common, with small sponges picked out by black manganese staining at 80.40m. A thin flint band at 80.85 to 80.95m comprises a medium sized, clean dark brown translucent flint with a thin, chalky patina. Fragments of *Inoceramus* at 81.30 and 82.00m. Below 82m, the chalk is greyish white, slightly marly, containing foraminifera and burrow structures. Bendekreide absent 82.00 to 83.15m, more coarsely grained below 83.30 and more abundant from 83..15 to 85.30m with black sulphide streaks(cf. pyrite or marcasite). Chalk then grade sinto a faintly yellowish marly chalk (eg. SAG 250, 251) with burrowfills and I*noceramus* fragments. Lithology coarsens below 86.35m. At SAG 256, the chalk is faintly greyish-white, gritty, many thick shelled *Inoceramus* fragments. Burrowfills at this interval displaced by up to 0.02m by a steeply dipping microfault at 88.10m. *Belemnitella langei* at 90.35-90.45m above a level where the core is cut by a series of conjugate sets of 60-70^{0} joints.

BELEMNITELLA MUCRONATA ZONE

PARAMOUDRA CHALK.

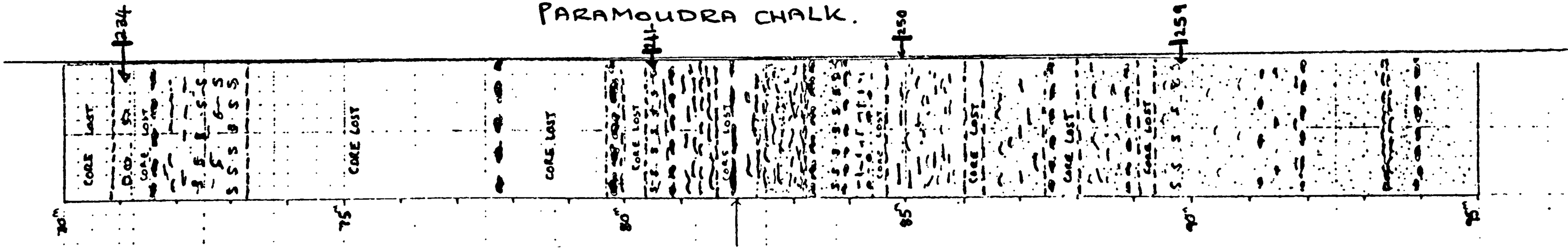
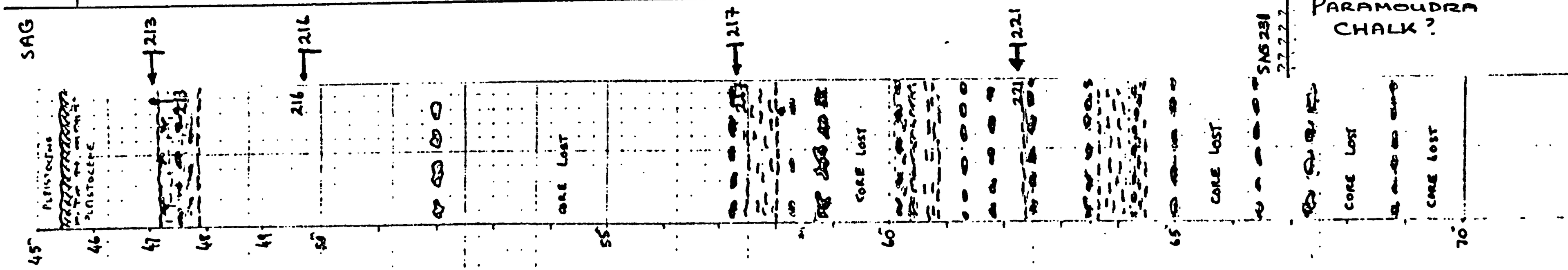


Fig. 1.8a.

BELEMNELLA LANCEOLATA. ZONE



At SAG 270 (96.40m) the chalk is massively bedded, with marl burrowfills and frequent fish debris. Jointing is rare. *Echinocorys* at 99.25m and a whole fish fossil; lithology alters to a creamy white fossiliferous chalk. Ammonites distinctive, preserved in moulds with "green skin". Flints either carious, dark brown or black centred with light grey cortex, or thalassinoid with black centres and white cortices. At 104.11m, the chalk is grey/white, marly, with abundant sponge fossils. Fossils include *Coelosmilia* and various gastropods. Abundance of marl burrows decreases, ammonite *Baculites* at 111.70m. At 112.50 (SAG 298) chalk contains a considerable amount of grey marly burrows, especially fossiliferous at a depth of 113.27-113.79 m, fossils include *Chlamys, Cretirhynchia, Echinocorys* and *Baculites.*

Upper Campanian *Belemnitella mucronata* Zone , Beeston Chalk, SAG 308-357, 122.45-156.38m.

The uppermost chalk of the Beeston Chalk beds is greyish-white, burrowed completely below 124.08m. There are two types of burrowfill; firstly, a large, diffuse burrowfill consisting of a blueish-grey Chalk, and secondly, a dark grey marly chalk fill. These are replaced by the more common grey marl burrowfill after 124.68m. Fossils sparce, although there is a thin bed (129.57-129.60m) with many small echinoderm ossicles and spines. A second fossiliferous band at 126.96 - 126.98m contains abundant gryphaeid, pycnodont and other oysters. A third bed (133.70 - 134.21m) with *Cardiaster, Magas, Cardium*, various oysters, echinoid spines, sponges and fish debris. There are few joints; lithology relatively constant; flints either thalassinoid (c. 120mm), small, lensoid (25mm) or of intermediate size (c. 80mm). Chalk is extensively burrowed, with some dislocation due to re-lithication or penecontemporaneous faulting. With increasing depth downcore, chalk becomes slightly darker in colour and is noticeably harder, although rock becomes softer and more earthy in texture below 132.98m. Associated fossills include *Inoceramus, Cretirhynchia, Echinocorys*. At 144.5m, lithology is much the same as in beds above, but texture is finely gritty, especially in some burrow concretions, possibly due to accumulation of foraminifera. Marly burrowfills are picked out by pale grey marl, probably preferentially orientated. An especially fossiliferous bed, beween 144.5 and 146.34 (e.g. SAG 345) passes into an earthy textured chalk with a lower marl content. A thin band of chalk (152-152.25m) is yellowish white and contains manganese stained sponges. The rock is moderately hard, grading into a grey-white, relatively fossiliferous chalk. Lensoid, complex, marly burrowfills show a chondritic appearance.

Figure 1.8b. illustrates the part of the Trunch Borehole log explained in the above text, down to 145m depth in the Beeston Chalk, represented in this study by sample SAG 345.

BELEMNITELLA MUCRONATA ZONE

BEESTON CHALK

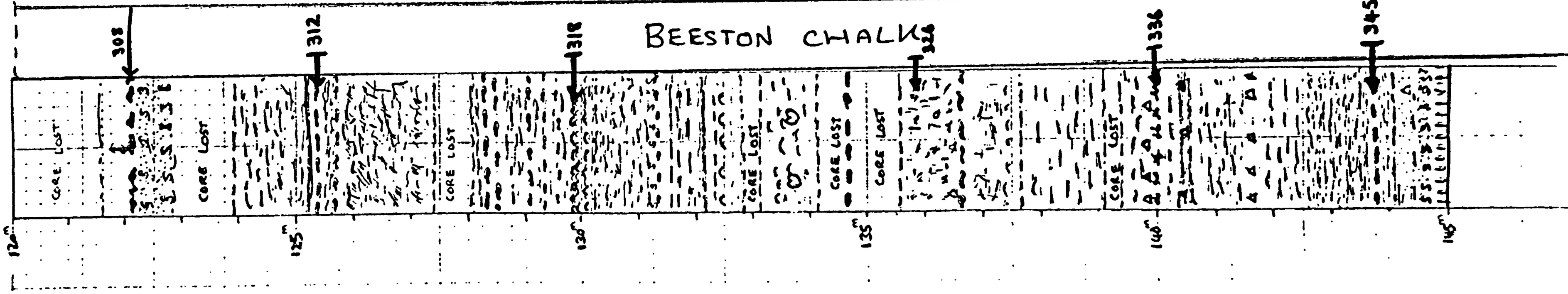
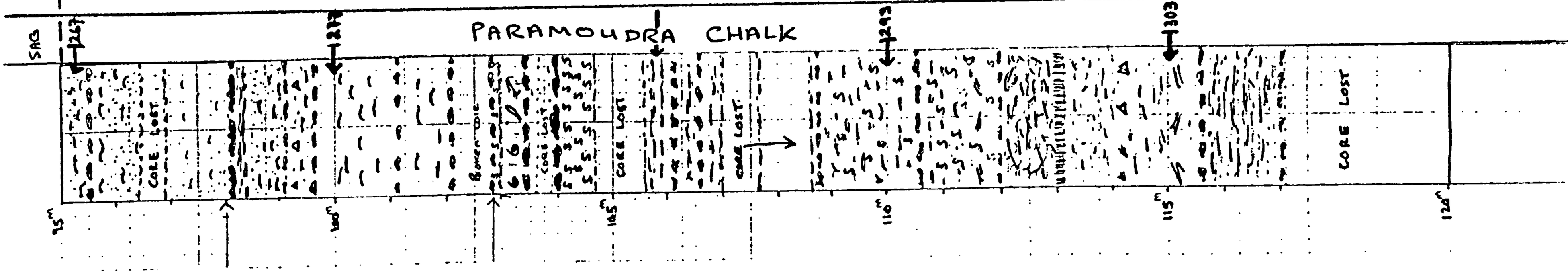


Fig. 1.8b.

BELEMNITELLA MUCRONATA ZONE

PARAMOUDRA CHALK



Upper Campanian *B. mucronata* Zone, Weybourne Chalk and basal *mucronata* Chalk - SAG 361-433, depth 156.95-209.07m:

The Weybourne Chalk is less gritty than the Beeston Chalk. It is a yellowish, grey-white rock, containing very large, complex, marly burrowfills up to 50mm deep. The unit itself is very fossiliferous, with *Porosphaera, Cretirhynchia, Magas, Chlamys, ?Salenia* and echinoids, asteroid ossicles and ostreid bivalves - *Cretirhynchia lenticularis*. Downcore, the lithology is constant but the texture becomes more marly. The genus *Kingenia* is mentioned in the BGS log and brachiopods e.g. *Terabratulina, ?Cardiotaxis* and *Orbirhynchia*.

In the lower beds of this unit, there are close sets of vertical and horizontal joints and the chalk is very fractured. After 190.38m, chalk is grey/white with faint, pale grey marly burrowfills and an earthy texture. Flints are generally of medium size (70mm) and are a dark, translucent brown with a thin cortex. The base of the Weybourne Chalk is hard and massively bedded, with a few scattered burrowfills (up to 3mm) and grey blotchy patches i.e. near hardground chalk. At 207.48 m, there is a U-shaped burrow with grey hardened edges. *Inoceramus* is abundant and occurs with calcitic bivalves, ostreids, serpulids, *Spondylus, Cardiaster.*

Lower Campanian, *Gonioteuthis quadrata* Zone, SAG 434 - 560, 09.17 - 272.47m depth:

The rock in this zone is initially similar to the basal *B. mucronata* Zone i.e. grey-white with yellowish to grey mottled patches - hardground challk. This grades into a browgrey-yellowish stained hard phosphatic surface grading down to hard, grey-white chalk with pale grey streaked marlt burrowfills (e. g. SAG 434, 435). The bed is fossiliferous, ontaining *Inoceramus, Cretirhynchia, Crania, Spondylus, Kingenia* and fish remains and calcitic bivalves. This is underlain by a bed which is fractured by strong vertical and slightly oblique horizontal jointing (c. 25^0 from horizontal). Some localised penecontemporaneous microjointing; oblique microfaults in complimentary sets (217.85 - 218.30m) and diamond jointing sets 60-120^0 from the vertical are recorded in the stratigraphical log. Flint medium sized with a black centre and pale grey, red-stained cortex, overlies thin layer of chalk which is more brittle with slightly fewer marly burrowfills. This is also strongly jointed. grading down into a thicker bed of grey-white chalk with abundant burrowfills (up to 50% of the rock, fossiliferous (SAG 453). After a core loss due to flint at 225.00m, chalk is grey-white with pale grey marly complex burrowfills, strongly jointed with predominantly vertical joints; secondary oblique jointing, diamond joints and irregular horizontal joints. This bed grades into massive chalk; few joints, very fossiliferous containing asteroid ossicles, terabratulids, echinoids, *?Micraster, Cretirhynchia, Neoflabellina,* fish remains and manganese stained sponges. The interval represented by SAG 473 is comprised of grey-white and white with white-light grey marly burrowfills which are generally streaked elongate horizontally. This is underlain by a bed of similar

lithology, poorly fossiliferous with a greater clay content than the beds above it. Fish debris lined burrows are common and fossils are generally more abundant below 231.40m; *Chlamys, Orbirhynchia*, Porosphaera, Neoflabellina, Echinocorys, Spondylus, Micraster, Coelosmilia, Cretirhynchia, *Chlamys concentricus & Neolithiothyrina.*

Concentrations of pale grey marly burrowfills with penecontemperaneous oblique microfaulting occur between 232.00 and 233.35 m. From 231.71 to 232.72, the chalk is moderately fossiliferous (SAG 474), containing *Neoflabellina, Echinocorys, Spondylus, Micraster* (e.g. *M. schroederi), Coelosmilia, Cretirhynchia,* Ostreid fragments and other small fossils. This bed then grades down (233.15- 233.45, represented by SAG 480) into a bed of white chalk with very pale grey marly burrowfills with a horizontal orientation. The rock is brittle, breaking with a sub-conchoidal fracture, and is less marly than the preceeding beds, but is fossiliferous (*Chlamys concentricus* at 233.28 m). It passes down into a thin band of massive, nodular flints with horizontal tops and rounded bases, 100 mm in size, with a dark grey to black centre and a thin, white chalky cortex stained (Fe?) at extremities. Underlying this is a thin (00.04m thick, 233.55 to 323.59 m depth) bed of white chalk with a similar lithology to the preceeding bed, but is much jointed with many vertical joints. A thin flint band grades down into a 00.69m thick (233.73 to 234.42m depth) grey/white chalk bed containing burrowfills up to 10mm thick, generally streaked horizontally; some complex and almost chondritic. The rock is earthy to rough textured, i.e. more clay content than the above lithology. Fossils are scattered and include *Echinocorys* plates, bryozoa, serpulids, terabratulids and calcitic bivalves such as *Chlamys* and *?Limea.* From 234.42 to 234.56 m depth), the chalk is white, with very pale grey marly burrowfills, and is gradational from the lithology above it, containing dark blue-grey sponge remains. The bed is fossiliferous with small terabratulinid and other fossil remains. A flint of medium size (100 mm), described in the BGS Trunch Borehole log as "roughly horizontal top surface, black centre with light grey grisly inclusions principally along the median part; thin, white chalky cortex stained dark grey / red brown at its extremities" grades down into a 1.64 m (234.66 to 236.60 m depth represented by sample SAG 484) chalk bed which is white with pale grey marly burrowfills, which may be chondritic. The lithology is similar to the bed above; earthy textured and brittle, breaking with a sub-conchoidal fracture. There is a break in the core below 235.61 m depth, probably because of the many irregular horizontal and vertical joint planes. At 235.00 m, a 50 mm horny thalassinoid burrow flint is recorded, with similar flints at 235.10 m and salt excressences on the exterior of the core from 235.15 m downwards. Medium sized thalassinoid burrow flints are recorded at 235.40 and 235.90 m. The bed is virtually barren of fossils but scattered fish remains are recorded, as well as *Orbirhynchia, ?Coelosmilia* and serpulids.

Below 236.30 is a thin layer (0.40 m) of grey / white chalk with medium and pale grey marly burrowfills, ramifying but many streaked with a preferred horizontal orientation, many complex and almost chondritic.

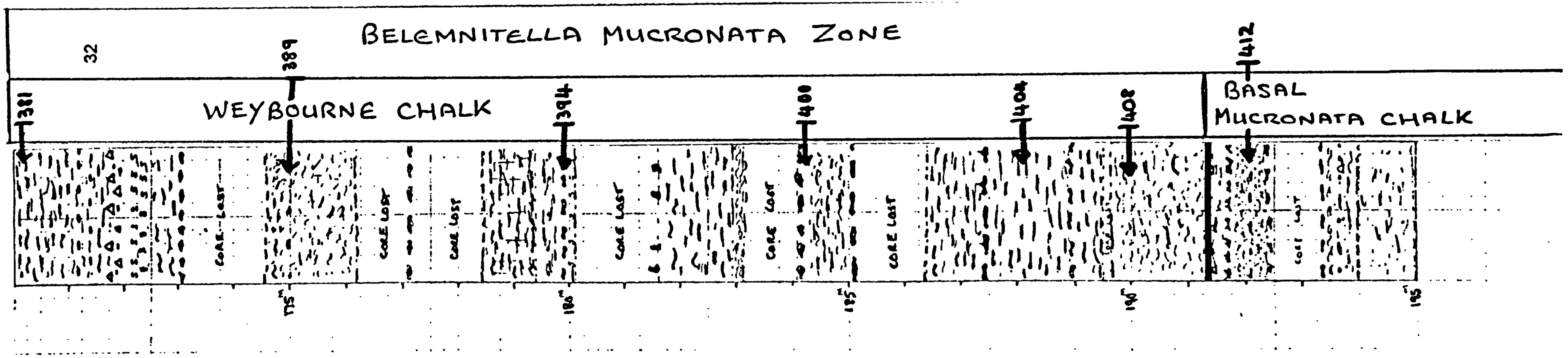
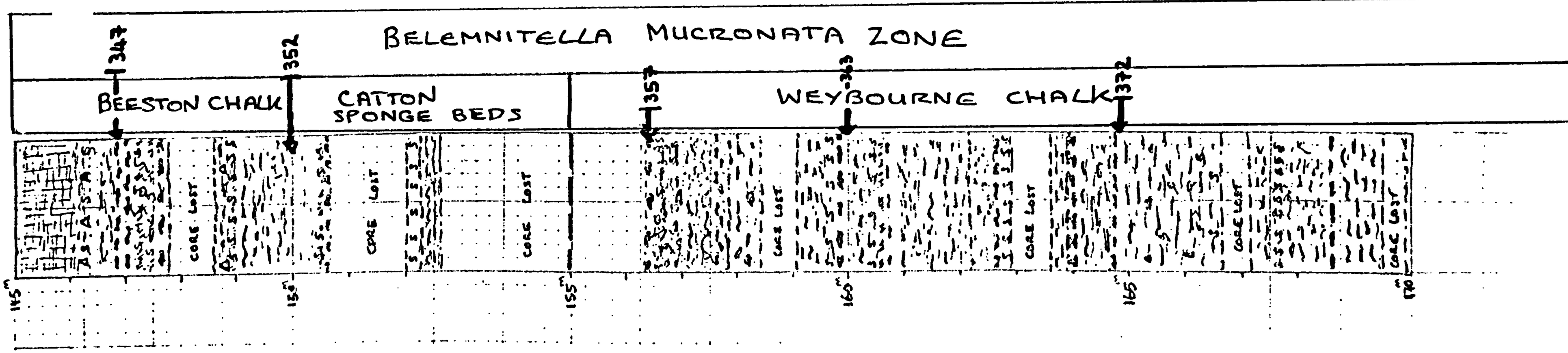

BELEMNITELLA MUCRONATA ZONE
WEYBOURNE CHALK
BASAL MUCRONATA CHALK
381
389
394
400
404
408
412
CORE LOST
175'
180'
185'
190'
195'

Fig. 1.8c.


BELEMNITELLA MUCRONATA ZONE
BEESTON CHALK
CATTON SPONGE BEDS
WEYBOURNE CHALK
347
352
357
363
372
CORE LOST
145'
150'
155'
160'
165'
170'

GONIOTEUTHIS QUADRATA ZONE

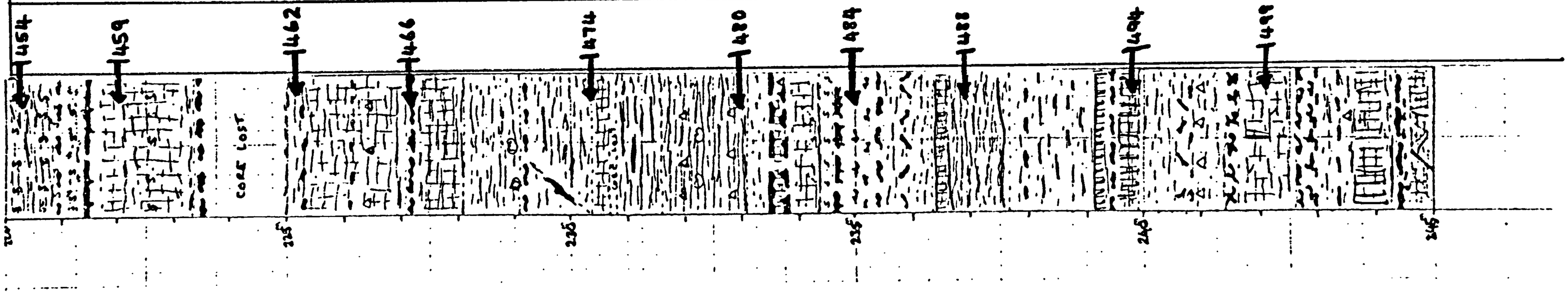
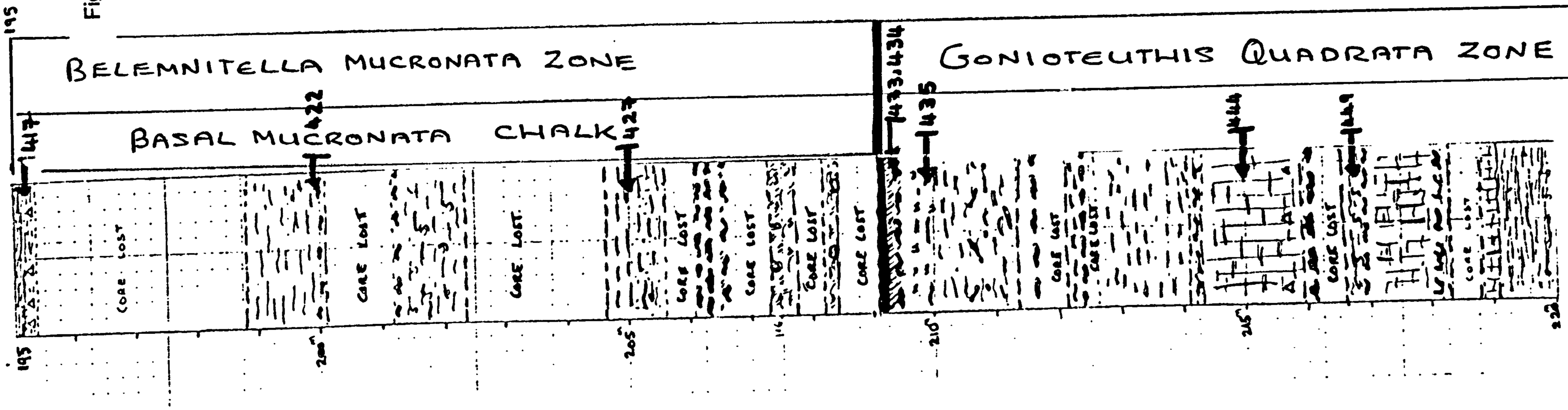


Fig. 1.8d.



The chalk is recorded as having a higher clay content than the above lithology, with a jointed zone between 236.30 and 236.57 m with strong vertical jointing and interesting irregular horizontal joints, strong vertical joint extends down to 236.45, where it is truncated by a horizontal joint. This bed is fossiliferous, with scattered and generally small fossils; fossils reasonably common below 236.79 with several fossil debris filled burrows. Between 237.70 and 239.46 m (SAG 488) is a 1.76 metre thick bed of white chalk with faint grey marly burrowfills not generally more than 10 mm thick. The chalk is earthy in texture and brittle, breaking with a subconchoidal fracture; massive with two horizontal joints and a complex jointed shattered zone below 239.16 to 239.43 m, with strong vertical jointing; a small 10 mm thalassinoid burrow flint at 237.94 m, a nodular flint at 238. 05 and a salt crust and excressences on the core. It is poorly fossiliferous, with scattered fossils, including cidarid radioles, asteroid ossicles, *Echinocorys* fragments, brachiopods, fish remains, *Terabratulina,* small coiled serpulids, *Gonioteuthis.* This grades into a 00.51 m (239.53 to 239.97 m depth) chalk bed with the same lithology as the chalk above it, but it is intensely jointed and almost barren of macrofossils. This grades into similar chalk, which is massive with few joints (1.51 metres thick; 239.97 to 241.48 m depth; SAG 494). Below 240.90 m, the core is broken with several sets of oblique diamond jointing; grading through a thin layer of flints set in fractured jointed chalk of the same lithology as above and then into a 0.92 m thick bed of white chalk (241.48 to 242.62 m depth; SAG 499), generally massive with vertical joints c. 80mm apart and fossiliferous, but the fossils are scattered and generally small. The chalk grades down through flints, small and medium size up to 80 mm and irregular, ramifying thalassinoid burrowflints, black centre, white and pale grey cortices, stained red-brown (Fe?) at top and bottom extremities, with some secondary brown crystal growth. The chalk between the flints is shattered and jointed; underlying the flints is a further 1.70 m of chalk with a similar lithology to much of the *Gonioteuthis quadrata* zone (242.74 to 244.44 m); irregular ramifying thalassinoid burrow flints recorded at 242.84 m extending 60 mm vertically (see BGS Trunch Borehole Log p. 44). At the base of this bed, the chalk is harder (from 244.00m) with a more conchoidal fracture. The bed is moderately fossiliferous, with the fossils generally scattered and comprising small *Inoceramus* fragments, echinoderm remains, fish debris, small serpulids. This bed of chalk is more fossiliferous below 243.87 m, with many asteroid ossicles, *Echinocorys, Orbirynchia* and *Gonioteuthis quadrata*. This grades down, through flints, into a thinner layer of chalk (00.79 m thick; 244.52 to 245.31 m depth; SAG 504) which is white with pale grey marly burrowfills, generally streaked horizontally and some complex burrows, and is earthy in texture, moderately hard with a sub-conchoidal fracture. Jointing is strong and the chalk is moderately fossiliferous, grading down into a further chalk bed (245.31 to 246.20 m depth) which is grey/white with large, complex, medium and pale grey marly burrowfills, often complex chondrites up to 70 mm thick; thin zoophycos type burrows at 245.92m picked out in medium grey marly chalk. Faulting is complex. Towards the bottom of the bed, the chalk is medium hard, rough textured and with less marl than the bed above it, with small, sinuous pyrite and marl filled burrows at 245.35 and 245.41m; moderately fossiliferous with asteroid ossicles, *Terabratulina* etc., and

dark grey pyrite preserved sponges at 245.46, 245.92 and 245.95 m depth. The chalk grades downwards through flint into a 00.61 m thick (246.23 to 246.84 m depth) chalk bed, which is grey-white with pale and medium grey, marly burrowfills up to 30mm thick, generally complex and chondritic, making up 30 % of the rock; these are cut by intense penecontemporaneous microfaults at 60 ^{o} and less to the vertical, producing an "almost pseudo-brecciated appearance. The chalk is poorly fossiliferous and grades into a grey-white chalk with faint pale grey marly burrowfills (e.g. SAG 508), generally small and laminar. The marl content is lower than in the above beds and this bed is moderately fossiliferous, overlying large flints which then grade downward into a 00.45 m chalk bed, flints and then a 00.47 m thick (248.11 to 248.58 m depth) bed of creamy grey/white chalk with indistinct pale grey marly burrowfills, which is poorly fossiliferous. A thicker (1.07 m; 248.58 to 249.65 m depth; SAG 512) bed of similar chalk underlies this but is more brittle, breaking with a sub-conchoidal fracture, with numerous joints; horizontal, oblique and predominantly vertical joints with thalassinoid burrowflints. This chalk is moderately fossiliferous, grading down through 00.95 metres of chalk (249.65 to 250.60 m depth; SAG 514), flints and then 00.79 metres of creamy grey/white chalk of a similar lithology, texture and fossil content to the chalk above it. The chalk below 251.51 m is of a similar lithology, but is fractured by many irregular joints and a small core loss at 252.07 m, with thalassinoid burrowflints, and a concentration of oysters between 251.94 to 251.94 m. Thalassinoid flints, zoophycos type laminae and horizontal marly burrowfills are common. From 251.51 to 254.20 m (SAG 520), the chalk is fossiliferous, with scattered asteroid ossicles, *Orbirhynchia*, fragments, brachiopods and echinoid fragments. Below a thin band of thalassinoid burrow flints at 254.20 to 254.22, a moderately fossiliferous bed of grey-white chalk and then from 254.77 to 255.18 m depth (SAG 524) into a 00.41 m thick grey-white chalk bed which is "transitional from the above lithology" and shows a decrease in the amount of grey marly burrowfills. Medium sized thalassinoid burrowflints grade into a creamy grey/white chalk which has indistinct pale grey marly burrowfills and zoophycos type laminae. A concentration of fossils is reported at 255.79 m depth (see BGS Trunch Borehole log, p. 53). This chalk is underlain by a 50 mm, medium sized lensoid burrowflint which, in part, fills a zoophycos type lamina of medium grey chalk. the flint grades down from 256.43 to 257.15 metres depth (represented by SAG 529), into a creamy grey-white chalk in which burrowfills make up less than 20 % of the rock; fossiliferous with scattered echinoderm remains and a concentration of fossils at 257.03 m. The chalk below this level and above the strong horizontal joint that marks the termination of the preceeding bed, is grey-white with pale and medium grey marly burrowfills which make up nearly 50 % of the rock, the zoophycos-type laminae are often dislocated by many vertical and oblique penecontemporaneous microfaults. Fossils are less abundant below 257.74 m with recorded fauna including *Terebratulina striata, Cretirhynchia intermedia, Echinocorys,* sponges and bryozoa.

Below a thin layer of thalassinoid burrow flints, the chalk is grey-white (258.00 to 258.70 m depth, 00.70 m thick), grading down into a thicker bed (1.60 m thickness; 258.70 to 260. 30 m depth,

represented by samples SAG 534). This bed of chalk is grey-white as above, with pale grey streaked burrowfills and medium grey zoophycos laminae which are often dislocated by penecontemporaneous microfaulting with scattered pyritised sponge remains at 258.61 m. Overall, this bed is poorly fossiliferous to 259.65 m, with scattered fish and dark grey sponges, and is more fossiliferous below 259.55 m, with gritty fossiliferous burrows and a varied fauna including *Kingenia, Orbirhynchia, Cretirhynchia, Gonioteuthis,* echinoderm fragments, *?Oxytoma,* dark grey sponge concretions at 260.03 m, with many fossils; bryozoans, serpulids and other bivalve remains. Underlying this bed, at 260.30 to 260.40 m, is a 100 mm thick flint, diagonally orientated, massive and nodular with a black to dark grey centre, thin chalky medium grey surface cortex, in part stained red-brown (Fe?). A 1.91 m thick (260.40 to 262.31 m depth) bed of white-grey chalk underlies the flint and is massive with few joints. Burrowfills are pale grey, marly thalassinoid and medium grey zoophycos laminae; the chalk itself is moderately fossiliferous with fish remains, echinoderms, brachiopods including *?Neoliothyrina, Orbirhynchia* and *Cretirhynchia*, serpulids, bryozoans, thin tested echinoids, bivalve fragments, *Inoceramus, Echinocorys, Spondylus* and dark grey sponge remains. The chalk is underlain by a band of nodular / "tabuloid" thalassinoid burrowflints up to 50mm thick, with adherant *Chlamys cretosa* at 262.32 m. The flints are underlain by a 1.36 m thick chalk bed (262.40 to 263.76 m depth, SAG 540) which is grey/white with complex chondritic pale grey marly burrowfills, thalassinoid and some zoophycos laminae picked out in medium grey marl. The chalk is recorded as having a greater marl content than the above beds and the core is broken between two horizontal joint planes at 262.53 to 262.72 m , otherwise the chalk is massive with few joints and moderately fossiliferous with echinoid radioles, serpulids and fish remains most common. Concentrations of fish remains are recorded at 262.59 m. Fossils are common below 262.80, with *Spondylus* and *Echinocorys.* Towards the base of this bed, the chalk is very marly (between 263.59 to 263.76 m depth), with complex burrowfill systems and many calcite filled, gritty cylindrical burrows, with a 15 mm lensoid flint. Below this is a 0.27 m thick band of lensoid, thalassinoid and nodular burrow flints with pale grey chalky cortices, stained (Fe?) at extremities, together with grey-white chalk with pale grey complex marly burrowfills. Towards the base of the *Gonioteuthis quadrata* Chalk, there is a noticable thickening in the chalk beds; thicknesses now range from 1.22 to 2.32 metres. The bed below the flints (264.03 to 265.25m depth, SAG 544) is a grey/white chalk, 1.22 m thick, with pale grey marly thalassinoid burrowfills, some complex and chondritic, generally streaked horizontally up to 20mm thick, with zoophycos laminae picked out in medium grey marl at 264.30 to 264.80 m and 265.00 to 265.14 m. The texture is earthy to rough, breaking with a subconchoidal fracture, and the chalk is massive with few joints, containing few fossils but many gritty calcite filled burrows. The bed grades down, through a double band of massive nodular flints, into a thicker bed of chalk with a similar lithology to the bed above (2.32 m thick; 265.52 to 267.84 m depth, represented by samples SAG 548, 549). There are few joints. Blue-grey calcite filled cylindrical burrows are common but the bed contains few fossils.

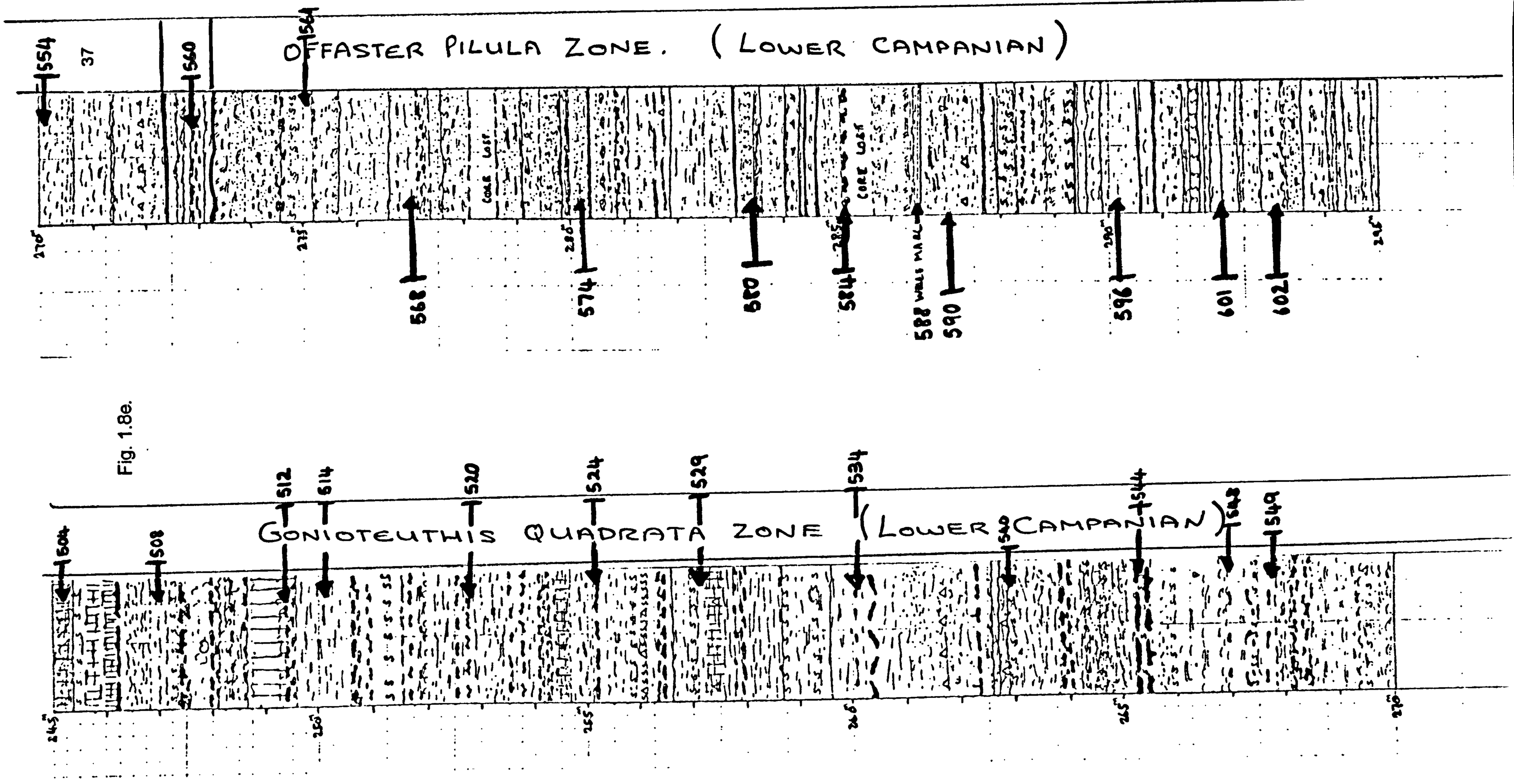

OFFASTER PILULA ZONE. (LOWER CAMPANIAN)
554
37
560
564
568
574
580
584
588 WELL MARK
590
596
601
602
GONIOTEUTHIS QUADRATA ZONE (LOWER CAMPANIAN)
504
508
512
514
520
524
529
534
540
544
548
549

Fig. 1.8e.

The chalk then passes into a thinner bed (0.21 m thick) of grey / white chalk with medium and pale grey complex marly burrowfills of thalassinoids and zoophycos laminae. The rock is described as "hard and brittle, with smooth and sub-conchoidal fracture; many thin marly partings almost stylolitic, about 10 mm apart forming a marly plexus with slabby chaks; dark grey sponge remains between 268.00 and 268.05; few other fossil remains." (p. 61 of the BGS Trunch Borehole log) The chalk from 268.20 to 270.49 m is 2.29 m thick and represented by samples SAG 554. It is recorded as grey-white to creamy with pale and medium grey zoophycos laminae and burrowfills dominant, together with complex burrowfills of thalassinoid type often chondritic. The chalk itself is medium hard, earthy textured breaking with a smooth to subconchoidal fracture. There are generally few joints but oblique "diamond" joints are recorded at several intervals. The chalk is locally hardened at 268.30 m with a hackly conchoidal fracture. Fossils are few, exept for scattered fish fragments and gritty cylindrical calcite filled burrows, grey sponge remains and *Inoceramus* fragments, *Gonioteuthis* at 269.37 m, *Chlamys cretosa* at 269.22 m. From 270.49 to 270.67 m, the chalk is transitional from the preceeding bed, with complex pale and medium grey marly burrowfills, but is hard, brittle "hackly" chalk, with a near conchoidal fracture; thin marly partings around 270.60 m, with some fossils including *?Kingenia;* the bed rests on a strong horizontal joint plane at 270.67 m. This transitional chalk grades into 1.75 m thick (270.67 to 272.47 m depth) grey/white and creamy chalk which is the terminal bed of *Gonioteuthis quadrata* zone Chalk. Burrowfills are pale and medium grey marl, often complex, chondritic and thalassinoid, with zoophycos laminae and burrowfills dominant. Penecontemporaneous microfaulting, attributed to compaction, is present throughout the bed, often with an oblique 60 ^{o} aspect, and the chalk is medium hard and earthy in texture, breaking with a sub-conchoidal fracture. Fossils are sparce. The bed is based by a strong horizontal joint plane at 272.47 m which marks the junction with the *Offaster pilula* zone Chalk.

<u>Zone 4</u> Upper Chalk - Lower Campanian *<u>Offaster pilula</u> zone :* (including the Wells Marl at 286.55 m) Depth: 272.47 to 306.72 m; samples SAG 560-629

The first chalk bed in this zone is 00.42 m thick (272.47 to 272.89 m depth) and is similar in lithology to the preceeding bed; pale and medium grey marly burrowfills make up about 30% of the rock and include zoophycos laminae, thalassinoid and chondritic burrow systems. The chalk breaks with a sub-conchoidal fracture, is generally massive, contains few joints and is fossiliferous - containing *Offaster pilula*, oyster fragments and fish and echinoderm debris. A thin belt of thin, 15 mm thick, elongate (up to 80 mm) ramifying thalassinoid burrowflints overlies a 00.95 m chalk bed (272.96 to 273.91 m depth, SAG 560) which is transitional from the bed above it and of a similar lithology, but is poorly fossiliferous, the chalk becoming gritty towards its base. The bed below is a 00.64 m bed of chalk, massive and transitional from above; grey / white to creamy white, with pale grey small chondritic marly burrowfills, and occasional medium grey streaked thalassinoid burrowfills making up less than 20% of the rock. The texture is earthy to rough, breaking with a poor-subconchoidal to irregular fracture.

Diagonal penecontemporaneous microfaulting is recorded, few joints are present and several flints (small elongate thalassinoid burrowflints, round nodular flints and larger thalassinoid / nodular flints - see BGS Trunch Borehole log p. 65) are recorded. The bed is fossiliferous and terminates on a strong horizontal bedding plane at 274.55 m. A 45 mm nodular flint was found on this bedding plane. Underlying this is a 1.18 m chalk bed (274.55 to 275.73 m depth; SAG 564) which is grey/white to creamy/white, with pale grey marly burrowfills of thalassinoid and chondritic type, making up less than 20% of the rock; earthy to rough texture, slightly gritty in top part, breaking with a smooth, sub-conchoidal fracture. The chalk is generally massive and fossiliferous with *Orbirhynchia, Inoceramus lingua*, echinoid remains, bivalve calcite fragments, dark grey sponge remains, serpulids and dark grey, gritty burrows. A medium sized individual of I*noceramus lingua* occurs on the upper surface of the strong horizontal joint plane at 275.73 m. This passes down into a fossiliferous 1.34 m (275.73 to 277.07 m depth) bed of chalk containing *Cidaris, Inoceramus, Gonioteuthis.*

From 277.07 to 277.31 m, a thin bed of grey/white creamy chalk is recorded, containing medium and pale grey marly burrowfills mainly of thalassinoid type, together with zoophycos and chondritic burrowfills making up 30% of the rock; tough earthy, gritty texture as before, breaking with an irregular to sub-conchoidal fracture with many diagonal penecontemporaneous compaction microfaults displacing burrowfills. This bed contains several thalassinoid burrowflints (see BGS Trunch Borehole log p. 67, 68) and is fossiliferous, with many fish and serpulid remains and cidaroid radioles and tests, *Inoceramus* fragments, dark grey sponge laminae, *Gonioteuthis* and oysters.

A 00.53 m section of the core was lost, from 278.13 to 278.66 m depth.

Below this, a 00.58 m thick bed of grey/white to creamy/white chalk extends from 278.66 to 279.24 m depth), with pale and medium grey marly burrowfills, of zoophycos and thalassinoid type, the latter type being more dominant in the upper part of the bed, but making up less than 25% of the rock. The texture is earthy-gritty in texture, with gritty burrowfills, breaking with a rough to subconchoidal fracture; fossils are few. The bed is underlain by a thinner (00.34m) bed of fossiliferous chalk, with medium and pale grey chondritic burrowfills together with abundant dark grey sponge remains, which is based by horizontal joint planes at 279.42 and 279.58 m depth. Between 279.58 and 280.00m, the chalk bed is 00.42 m thick and the rock is creamy white to grey/ white, especially in the lower part, with pale and medium grey marly burrowfills, chondritic in upper part and thalassinoid in lower part forming a marly burrowfill concentration. The texture is earthy, gritty especially in lower part of bed, breaking with an irregular uneven fracture; chalk fossiliferous with cidarid radioles and plates, *Gonioteuthis*, grey sponge remains, *?Craticularia, Inoceramus, Oxytoma* and *?Neoflabellina*. A thin (00.29 m thick) bed of chalk underlies the preceeding bed; creamy grey white with medium grey marly burrowfils of chondritic or zoophycos type making up less than 25 % of the rock, with a earthy gritty texture, breaking with a rough - subconchoidal fracture and fossiliferous. This bed grades down through a 20mm tabular flint into a 00.22 m thick bed of chalk rubble of similar lithology to the preceeding bed, containing loose 40mm nodular

carious flint. Between 280.54 and 280.81 m (SAG 574) the chalk is 00.27 m thick, white with medium grey zoophycos type marly laminae which make up less than 10 % of the rock, breaking with an irregular subconchoidal fracture. The bed is massive, with few joint planes; fossiliferous with calcitic bivalves including *Inoceramus* and *Oxytoma*, together with echinoid radioles. A bed of roughly equal thickness follows (280.81 to 281.10 m depth), comprised of fossiliferous chalk; white and grey-white with medium and pale grey marly zoophycos and thalassinoid burrowfills, generally elongated horizontally. The bed is transitional into a 00.86 m thick (281.10 to 281.96 m depth) bed of white and grey white chalk with medium and pale grey marly burrows of zoophycos type; generally horizontally elongate. The texture is described as firm and earthy, breaking with a smooth to subconchoidal fracture; a horizontal joint is recorded at 281.28 m (see BGS Trunch Borehole Log, p. 72). The bed is fossiliferous, with fish remains and calcitic bivalves including large oysters, *Oxytoma, ?Spondylus, ?Parasmilia, Offaster, Inoceramus* and others, and terminates on a strong horizontal joint plane at 281.96 m with adjacent hardened chalk. A thicker (1.17 m, 281.96 to 283.13 m depth; SAG 580) bed underlies this; white chalk, massive and poorly fossiliferous with a subconchoidal to hackly fracture, with pale grey and medium grey marly burrowfills largely thalassinoid and chondritic, with some zoophycos type making up less than 15 % of the rock, oblique, penecontemporaneous microfaulting is recorded 45 to 60 ^{o} to vertical displacing marly burrowfills throughout, horizontal bedding plane recorded at 282.76 m (see BGS log, p. 72), bed terminated by a strong horizontal joint plane at 283.13 m depth. Below this (283.13 to 283.61 m depth; 00.48m thickness) is a further bed of white / creamy chalk with pale and medium grey marly burrowfills which are predominantly of zoophycos type laminae and make up less than 10 % of the rock. The texture is firm, earthy, gritty; breaking with a subchonchoidal fracture. The bed is generally massive, with few joints, a horizontal joint plane at 283. 37 m, and contains scattered fossils remains including fish fragments, *?Offaster,* grey-blue sponge remains and a bed of *Inoceramus* at 283.60 to 283.61 m. The core then passes through a 00.15 m band of thalassinoid burrowflints, horizontally lying Y shaped at 283.63m up to 34mm thick, into a 00.94 m (283.76 to 284.70 m depth) thickness of creamy/white chalk with pale and medium grey marly burrowfills, predominantly of zoophycos and chondritic type making up less than 10% of the rock. The rock itself has a firm earthy-gritty textured (less gritty downcore), breaking with a subconchoidal fracture, and is generally massive with a few horizontal joints and many oblique penecontemporaneous (compaction) microfaults at 45-60degrees to the vertical, forming "diamond, imbricate structure in places". Thalassinoid flints are recorded at several intervals and fossils are scattered, including fish debris and *Inoceramus* chips, *?Kingenia,* serpulids, *Chlamys cretosa, Offaster,* etc. The bed is terminated by a horizontal joint plane at 284.70 m.

A 00.44 m thick bed of massive, sparcely fossiliferous chalk (e.g. SAG 584) lies below the joint plane; creamy white and similar in lithology to the bed above it, with pale and medium grey marly burrowfills predominantly of thalassinoid type and making up less than 10% of the rock, which has an earthy, slightly gritty texture and breaks with a subconchoidal fracture.

The bed below the massive 100mm nodular flint and the 00.47 m of core loss is 00.79 m thick (285.70 to 286.49 m depth); creamy white, massive and medium hard, earthy-gritty textured chalk with occasional medium grey marly burrowfills of zoophycos type laminae. The rock breaks with a subconchoidal to uneven fracture and is tough and harder below 286.20 m with an abrasive texture and gritty burrowfills at 286.31m depth. The bed is fossiliferous with sponges, scattered fish remains, *Inoceramus* beds and some dark grey pyritic trails. The bed is very tough at its base, grading into a thin bed of grey/green laminated marl (the Wells Marl) at 286.49 to 286.55 m, with darker grey streaks; the probable equivalent of the thick marl in the Wells Chalk Pit. The Wells Marl is underlain by a 1.23 m thick bed (286.55 to 287.78 m depth; SAG 590) of creamy white, massive, earthy textured (schreibekreide) chalk, which is slightly gritty in parts and breaks with a rough to subconchoidal fracture. A horizontal joint plane and many oblique compaction penecontemporaneous microfaults are recorded (see BGS log, p. 75), as are small calcite filled cylindrical burrows. The bed is fossiliferous with fish remains, *Inoceramus* fragments, bryozoa and small brachiopods including *Terabratulina, Orbirhynchia,* calcitic bivalves such as *Chlamys* and *Gyropleura,* asteroid ossicles, small brachiopods and *Offaster.* Below a 25mm tabular flint with attached *Terabratulina*, two thin beds of fossiliferous chalk (00.15, 00.31m in depth respectively) grade into a 1.15 m thick (288.26 to 289.41m depth) bed of creamy white chalk which contains scattered pale grey marly burrowfills of chondritic and thalassinoid type with occasional medium grey burrowfills of zoophycos type. The rock has a firm, earthy texture, is massive with few joints and breaks with a smooth and subconchoidal fracture. Frequent penecontemporaneous microfaulting is recorded, along with abundant thalassinoid burrowflints (see BGS Trunch Borehole log, p. 76). At 289.22 m depth, there is a greater marl content, with many burrowfills. The bed is fossiliferous, containing fish remains, small oysters, small brachiopods including *Orbirhynchia, Inoceramus,* serpulids, regular echinoid, and is terminated by a strong horizontal joint plane. A 1.38 m thick poorly fossiliferous chalk bed underlies this joint plane; creamy white with scattered pale grey and medium grey marly burrowfills, predominantly of thalassinoid and chondritic type making up less than 10 % of the rock; firm/ medium hard, earthy in texture and breaking with a smooth to subconchoidal fracture. A thinner poorly fossiliferous chalk bed lies at 290.81 to 291.50 m depth (00.69m thick). The rock is creamy white with faint pale grey marly thalassinoid type burrowfills, with medium grey horizontal marly burrowfills of chondritic and zoophycos type, making up less than 10%. A thin (00.10 m) bed of similar chalk lies below this, containing abundant dark grey pyritic sponge remains, together with large 15mm complex marly burrowfill of zoophycos / chondritic type and sponge laminae.

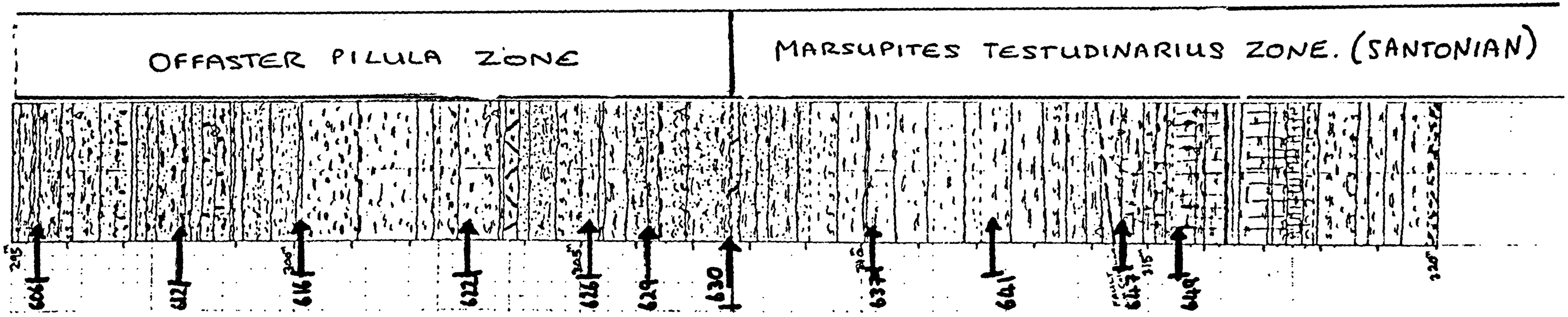
The 00.90m thick bed at 291.60 to 292.50m depth comprises massive creamy white chalk with faint light grey mottling of pale grey marly thalassinoid type burrowfills, together with medium grey marly burrowfills of zoophycos and chondritic type, oblique horizontal and vertically orientated and making up less than 10% of the rock. Three horizontal joint planes are recorded in the BGS log; fossils are few and scattered. A thicker bed (1.12 m thick; 292.50 to 293.62 m depth; SAG 601) underlies the preceding bed, consisting of creamy white poorly fossiliferous chalk with faint pale grey mottling of thalassinoid

burrowfills and small grey burrowfills of zoophycos and chondritic type making up less than 10% of the rock. From 293.62 to 296.14 m (SAG 602, 606), the 2.52m thick chalk is rather similar to the bed above but containing large complex burrowfills up to 50 mm across, predominantly of chondritic and zoophycos type, making up less than 20% of the rock. Texture is noted as firm, earthy, slightly gritty, breaking with an uneven to subconchoidal fracture. Fossils are few and scattered. Frequent horizontal joint planes are recorded, often associated with adjacent hardened chalk. A strong horizontal joint plane at 296.14 m marks the base of the bed. Below the joint plane is a 0.93 m thick (296.14 to 297.07 m depth) massive bed of creamy white chalk, with faint pale grey marly thalassinoid burrowfills and medium grey burrowfills of chondritic and zoophycos type, with greater amounts of chondritic type fills towards the base; making up less than 15 % of the bed. Texture is described as earthy and slightly gritty, breaking with an irregular to subconchoidal fracture. The bed is fossiliferous (oysters, *Inoceramus,* fish, *Echinocorys, Bourgueticrinus, ? Offaster*) and based on a strong horizontal bedding plane at 297.07 m depth.

The bed below the joint plane (1.28 m thick; 297.07 to 298.35m; SAG 612) comprises massive creamy white chalk with faint pale grey mottling of thalassinoid type marly burrowfills and with well defined medium grey marly burrowfills of chondritic and zoophycos type; making up about 20% of the rock, which is medium hard, earthy gritty and abrasive in texture, breaking with a smooth, irregular to subconchoidal fracture. A few joints are recorded (see p. 81 of BGS log), as are complex oblique penecontemporaneous (compaction) microfaults. The bed is fossiliferous, containing fish remains, abundant *Inoceramus* chips and oysters, *Gonioteuthis, Orbirhynchia.* A thicker bed of chalk (1.82 m thick) lies below this at 298.35 to 300.17 m depth; creamy white with faint pale grey marly burrowfills of thalassinoid type, and more strongly defined medium grey marly chondritic and zoophycos burrowfills making up less than 15 % of the rock, which is medium hard and has an earthy slightly gritty texture. The bed is generally massive with few joints, with 7 horizontal joint planes recorded in the BGS log (p. 82). Many small calcite filled cylindrical burrows are present throughout with gritty bands at 299.31 to 299.50, around 299.67 m, with gritty calcite filled burrows around 300.14 - just below the strong horizontal joint plane that terminates the bed. Fossils are reasonably abundant, including *Inoceramus, Cardiaster, Kingenia,?Belemnitella,* asteroid ossicles, oysters, fish debris and bryozoa.

The lithology of the bed below is transitional (0.99 m thick; 300.17 to 301.16; SAG 616); creamy white chalk, shelly with oysters and scattered medium grey zoophycos marly burrowfills. Burrowfills are generally elongate horizontal, making up less than 10 % of the rock, which breaks with a smooth to irregular fracture and is massive with few joints. Calcite filled cylindrical burrows are common throughout and flints are also recorded at several intervals. The bed is very fossiliferous but with "limited fauna of *Ostrea* of 'Boucheroni' type, *Inoceramus* sheets, *Orbirhynchia* and cidarid radioles; bed based on strong horizontal plane at 301.16" (p. 83). A 30 mm nodular / tabular flint lies below the strong joint plane, overlying a 0.88 m thick (301.19 to 302.07 m depth) bed of similar chalk with horizontal joint planes at 301.32m and 301.47m with broken core between. Oysters are less common than above.

Fig. 1.8f.


OFFASTER PILULA ZONE
MARSUPITES TESTUDINARIUS ZONE. (SANTONIAN)
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The bed is transitional and similar to the 1.58 m bed of underlying chalk (302.07 to 303.65 m; SAG 622), which differs in the presence of chondritic as well as zoophycos type burrowfills making up less than 10% of the rock. The rock breaks with a smooth to subconchoidal fracture and is fossiliferous. Below a thin bed of chalk; a 00.18 m thick broken section of core comprising chalk and based by a strong horizontal joint plane, is a thicker (0.69 m, 303.83 to 304.52 m depth) bed of creamy white massive fossiliferous chalk with a few irregular vertical diagonal and horizontal joint planes with a strong horizontal joint plane at 304.12 m and many small cylindrical calcite filled burrows. Burrowfills in this bed are medium grey marly zoophycos and chondritic type becoming more frequent downwards, and complex gritty calcite filled burrows making up 15 to 20 % of the rock, which is medium hard, very gritty earthy textured, and breaks with a smooth to subconchoidal fracture. Between 304.52 to 306. 43m (represented by SAG 626; 1.91 m in thickness), the rock is creamy white chalk, with faint grey background mottling of thalassinoid type, and medium grey burrowfills of chondritic and zoophycos type; generally elongate horizontally but with some vertical burrowfills; often complex, up to 25 mm thick and making up to 25 % of the rock. The log (p. 85) records the bed as firm to medium hard earthy, slightly gritty in texture, breaking with a smooth to subconchoidal fracture and "essentially massive but with many sets of 60 ° diamond joints such that the core was broken below 305.30 m", 5 horizontal and two vertical joint planes are recorded. Blue grey small calcite filled cylindrical burrows are common throughout, with gritty burrowfills common below 305.88, and the bed is fossiliferous, lying immediately above a 30mm lensoid tabular flint containing secondary vertical fractures filled with ?calcite. Below the flint, the last bed (c. bed 45) of the *Offaster pilula* zone Chalk is a thin bed of fossiliferous white and grey white chalk with blue grey gritty calcitic burrowfills with pyrite common, up to 20 mm thick. The texture is earthy -gritty/abrasive, breaking with an irregular to subconchoidal fracture. Zoophycos type laminae are recorded towards the base of the bed which terminates at 306.72 on a "burrowed junction" (see BGS Trunch Borehole log, p. 86).

Santonian *Marsupites testudinarius* Zone SAG 630-648, depth 306.72-319.88m

The first bed of the *Marsupites testudinarius* Zone Chalk (306.72 to 309.05, represented by SAG 630) is 2.33m thick, comprising creamy white chalk with medium grey marly burrowfills of zoophycos and chondritic type generally aligned horizontally, some complex or gritty calcite burrowfills, all not making up more than 15% of the rock, which is slightly gritty in texture, breaking with an irregular to subconchoidal fracture. The bed contains few joint planes, penecontemporaneous microfaulting is present; irregular and branching between 306.95 to 307.85m, from near vertical to 60 ° and 20-60° simiple microfaults between 308.30 and 307.85m; small calcite and pyrite filled cylindrical burrows present throughout. The bed is fossiliferous, with *Inoceramus* chips and oysters, *Porosphaera, Echinocorys* and associated asteroid ossicles, *Marsupites* at 307.35m, *Orbirhynchia*. The bed is underlain by a 2.71m bed of creamy white chalk (309.05 to 311.76m, SAG 637). Burrowfills are faint pale grey thalassinoid type, medium chondritic and with occasional zoophycos making up less than 10% of the rock, which has a firm, earthy, schreibkreide texture and breaks with a smooth to sub-conchoidal fracture. 6 horizontal joint planes are recorded (p. 87 of the BGS log), diagonal penecontemporaneous microfaulting is present throughout, 40-60° almost imbricate in places. The bed is fossiliferous, but with scattered fossils including oysters, *Kingenia lima, Orbirhynchia, Gonioteuthis, Marsupites, Terabratulina striata* and others. The core is

broken between 311.76 to 312.18, with a slight core loss from 312.60 to 312.18. Below this, is a 2.22m bed of chalk which is similar to the bed above but with larger zoophycos and chondritic medium grey marly burrowfills up to 20mm thick, generally elongate horizontally and making up 15% of the rock, which breaks with smooth to subconchoidal fracture. 5 horizontal joint planes are recorded, along with 60° diamond (diagonal) joints below 313.75. Small cylindrical calcite filled burrows present throughout, with occasional gritty bands becoming more frequent downwards. The bed is poorly fossiliferous. A fault plane is recorded in the BGS Trunch Borehole log (p. 89); an oblique 55° Hade normal fault with strong slickensides and a "vein of crystalline Celestine up to 6mm thick."" Below the fault, a 1.28m bed of crea,my white chalk shows faint grey marly burrowfills of thalassinoid type but is dominated by medium grey marly burrowfills of chondritic and zoophycos type with horizontal and vertical orientation, making up c. 15% of the rock. The bed is a firm earthy textured schriebkreide and is generally herder next to the fault plane, breaking with a smooth to subconchoidal fracture. 4 horizontal joint planes are recorded, together with several burrowflints and the occasional gritty burrowfill. The bed itself is poorly fossiliferous wioth scattered cidarid radioles, echinoid, oyster and *Inoceramus* fragments, ?*Kingenia, Spondylus, ?Marsupites*. Dark grey sponges are recorded at the base of the bed below 315.42m.

The fifth bed of the *Marsupites* Zone Chalk (315.47 to 316.27 depth, 0.80m thick) is represented by SAG 649. It is similar to the bed above but is much more fossiliferous and has pale and medium grey marly horizontal burrowfills of zoophycos type and some subsidiary chondrites, making up c. 10% of the rock. A thin 7mm to 10mm tabular flint underlies the 5th bed, overlying a 1.58m thick (316.28 - 317.86m deth) bed of creamy white chalk with faint grey marly burrowfills, generally 10mm thick, elongate horizontally, of zoophycoos type with subsidiary chondrites which both make up 10% of the rock. The bed is essentially massive but has many joint planes; 6 horizontal and strong vertical joint planes recorded, Unlike the preceeding chalk, this bed is poorly fossiliferous, with scattered echinoderm remains and small brachiopods, *Kingenia?, Marsupites*, fish remains, asteroid ossicles and oysters, dark grey sponge remains.

The last bed recorded on the BGS log (p. 91) between 317.86 and 319.88m depth is a 2,02m thick bed of grey/white chalk which shows a noticable change in lithology. Burrowfills consist of faint medium grey marly thalassinoid type burrowfills and medium grey marly zoophycos and chondrite fills, all of which make up 50% of the rock. Texture is described as firm, earthy, breaking with a smooth to subconchoidal fracture. The bed is massive, with few joints. 5 horizontal joint planes are recorded, with penecontemporaneous microfaulting common throughout. The bed is fossiliferous, but with generally scattered echinoderms, small, thin-shelled oysters and occasional *Inoceramus* chips, ?*Parasmilia*, dark grey sponge remains, *Porosphaera, Marsupites*and others.

Table 1.7. Trunch Borehole samples and their equivalents

Trunch Borehole	subdivisions	Zone	substage	outcrop samples
	Grey Beds	*Belemnella lanceolata*	Lower Maastrichtian	SAG 2010-2006
	Ostrea lunata Chalk			SAG 2001 - 2005
SAG 213, 216	*Porosphaera* Beds			SAG 2018 - 2019
SAG 217, 221, 231	pre-*Porosphaera* Beds			SAG 2013 - 2017
SAG 241 - 308	Paramoudra Chalk	*Belemnitella mucronata*	Upper Campanian	SAG 66, 111, 112 83 - 77
SAG 312 - 345	Beeston Chalk			SAG 13, 51 - 58
SAG 357	Weybourne Chalk			SAG 99 - 105, 59 - 61, 151-154, 20-24, 6-12
	Eaton Chalk			SAG 92 - 98
SAG 363 - 433	basal *mucronata* Chalk			SAG 67, 68, 106-110 170, 84-91
SAG 434 - 560		*Gonioteuthis quadrata*	Lower Campanian	SAG 202, 201, 38-34 SAG 186-189, 44, 45, 25, 26, 27, 28, 29
SAG 568 - 629		*Offaster pilula*		SAG 30, 31, 32, 33
SAG 630 - 648		*Marsupites testudinarius*	Santonian	SAG 43, 199
		Uintacrinus		SAG 73
		high *coranguinum*		SAG 14, 15, 47 - 50
		coranguinum	Coniacian	
		low *coranguinum*		
		basal *coranguinum*		

Table 1.8. Outcrop localities and grid references - Lower Maastrichtian samples.

sample	age	zone	locality	grid reference
1, 2, 3, 4, 5,	Lower Maastrichtian		Sidestrand, Norfolk, cliff section, site of Overstrand hotel	TG 253 408
62, 63, 64, 65	Lower Maastrichtian	see p. for divisions	Trimingham, Norfolk, cliff section, Bluff at little Marl point	TG 298 379
69	Lower Maastrichtian	"Western Mass"	Sidestrand, Norfolk, cliff section	TG 255 404
70, 71	Lower Maastrichtian	"central mass"	Sidestrand, Norfolk, foreshore exposure	TG 255 404
2001, 2002, 2003, 2004, 2005	Lower Maastrichtian	*O. lunata* Chalk- see p. for divisions	Trimingham, Norfolk, Marl Point, overturned foreshore mass-	TG 293 841
2006, 2007, 2008, 2009, 2010, 2011	Lower Maastrichtian	Grey Beds, samples 1 to 6	Trimingham, Norfolk, Marl Point, reversed dip mass, foreshore exposure	TG 293 841
2012	Lower Maastrichtian	Grey Beds	Trimingham Norfolk, Little Marl Point	TG 297 3809
2013, 2014, 2015, 2016	Lower Maastrichtian	pre-*Porosphaera* Beds	Sidestrand, Norfolk, western mass - upper monocline	TG 2570 4038
2018, 2019	Lower Maastrichtian	*Porosphaera* Beds	Sidestrand, Norfolk, western mass, cliff section	TG 25704038
2050	Lower Maastrichtian	Grey Beds	Trimingham, Norfolk, Marl point	TG 29233841
2051	Lower Maastrichtian	Grey Beds - equates stratigraphically with SAG 2006 - 2012, 2050	Mundesley no. 1 Borehole, Mundesley, Norfolk; depth 44 to 45' 6"	TG 317 364
2052	Lower Maastrichtian	Grey Beds - equates stratigraphically with SAG 2006 - 2012, 2050	Mundesley no. 1 Borehole, Mundesley, Norfolk; depth 46' to 47' 6"	TG 317 364
2053	Lower Maastrichtian	Grey Beds - equates stratigraphically with SAG 2006 - 2012, 2050	Mundesley no. 1 Borehole, Mundesley, Norfolk; depth 47' 6" to 49'	TG 317 364

Table 1.9. Outcrop localities and grid references - Upper Campanian samples.

sample	age	zone	locality	grid reference
13	upper Upper Campanian	top Beeston Chalk	West Runton, foreshore, Norfolk	TG 188 434
20, 21, 22, 23, 24	upper Upper Campanian	overlap with and continuation of Catton Grove (SAG 6-12)	Stoke Holy Cross, Norfolk	TG 233 026
40, 41, 42	upper Upper Campanian	Beeston Chalk	Frettenham, Norfolk	TG 246 172
51, 52, 53, 54, 55, 56, 57, 58	upper Upper Campanian	Beeston Chalk	Caistor St. Edmund, quarry, Norfolk	TG 239 048
66	uppermost Upper Campanian or basal Lower Maastrichtian	"Lower Mass"	Sidestrand, Norfolk, Cliff section, site of Overstrand Hotel (same locality as SAG 1)	TG 253 408
77, 78, 79, 80, 81, 82, 83	topmost Upper Campanian	Paramoudra Chalk - see p. for divisions	SAG 77 - 82 Crown Point Pit, Whitlingham, Norfolk; SAG 83 Church Pit, Whitlingham, Norfolk	SAG 77 -82 TG 267 077; SAG 83 TG 273 078
111	uppermost Upper Campanian	Paramoudra Chalk	Tollgate Pit, Thorpe, Norfolk	TG 283 089
112	upper Upper Campanian	Paramoudra Chalk	Asylum Pit, Thorpe, Norfolk	TG 275 089
179	upper Upper Campanian	basal Eaton Chalk, basal *mucronata* zone; probably equivalent to Furze Hill (SAG 76) and possibly Cley-next-the Sea (SAG 46)	Cringleford, nr. Norwich, Norfolk - pit to NE of Newfound Farm	TG 189 069

Table 1.9. Outcrop localities and grid references - Upper Campanian samples (continued).

sample	age	zone	locality	grid reference
6, 7, 8, 9, 10, 11,12	top of lower Upper Campanian , base of upper Upper Campanian		Catton Grove, quarry, Norfolk	TG 229 109
59, 60, 61	lower Upper Campanian ,	Weybourne Chalk	Weybourne, Norfolk, cliff section	TG 110 438
67, 68	lower Upper Campanian		Cringleford, Norfolk	TG 203 063
75	lower Upper Campanian	yellow Chalk sample from top of section	Rowe's locality 190, south of Flordon Church, Norfolk	TM 189 972
76	lower Upper Campanian	basal *mucronata* Chalk	Rowe's locality 49, Furze Hill, between Tasburgh and Tharston, Norfolk	TM 193 956
84 to 98 inclusive	lower Upper Campanian	type locality of Eaton Chalk, lower half of *mucronata* Chalk	Eaton, Norfolk	TG 208 064
99, 100, 101, 102, 103, 104, 105	lower Upper Campanian	Middle Weybourne Chalk	Keswick, Norfolk	TG 215 048
106, 107, 108, 109, 110	lower Upper Campanian	*mucronata* zone Chalk	Cringleford, Norfolk	TG 197 059
136	lower Upper Campanian	Eaton Chalk, *mucronata* zone	Drayton, nr. Norwich, Norfolk	TG 174 132
151, 152, 153, 154	lower Upper Campanian	*mucronata* zone, Upper Weybourne Chalk	Eaton, Norfolk	TG 219 058
180	lower Upper Campanian	basal *mucronata* zone Chalk	Bowthorpe, Norfolk	TG 176 091

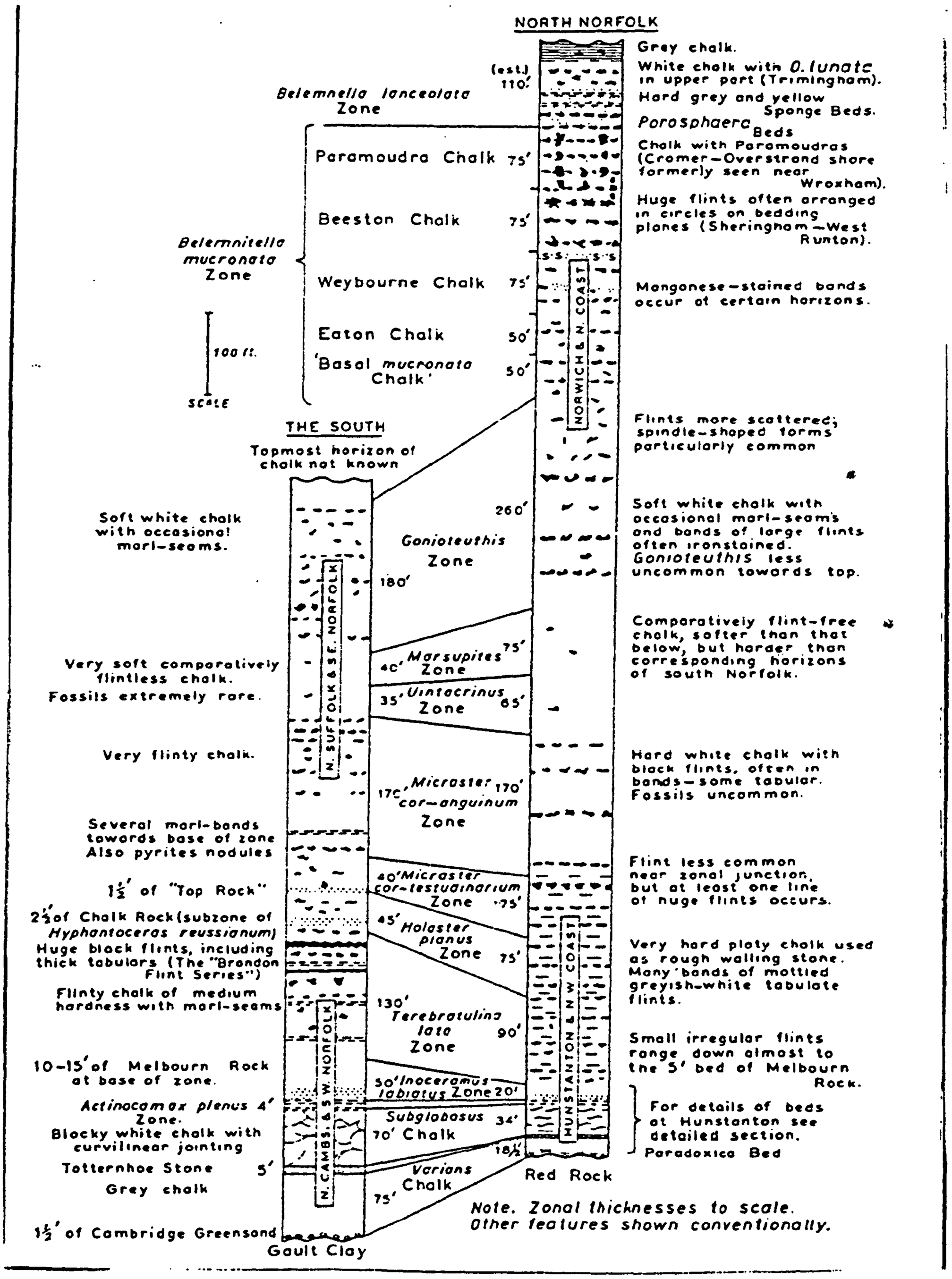
Table 1.10 - Outcrop localities and grid references - Lower Campanian samples.

samples	age	zone	locality	grid reference
25, 26, 27	Lower Campanian	restricted *quadrata* zone	Stiffkey,Norfolk, Locality 1 - yard of Hall Farm	TF 975 428
28, 29	Lower Campanian	restricted *quadrata* zone	Stiffkey,Norfolk, Locality 2 - quarry	TF 971 429
30, 31, 32	Lower Campanian	probably *pilula* zone	Wells, Norfolk - quarry	TF 928 429
33	Lower Campanian	*pilula* or lower part of restricted *quadrata* zone	Wells, Norfolk	TF 928 429
34, 35, 36, 37, 38	Lower Campanian	probably lower part of restricted *quadrata* zone	Wells, Norfolk	TF 928 429
44, 45	Lower Campanian	restricted *quadrata* zone	Alderford Common, Norfolk	TG 129 183
181	Lower Campanian	topmost restricted *quadrata* zone	Bawburgh, Norfolk	TG 149 088
182	Lower Campanian	topmost restricted *quadrata* zone (upper Lower Campanian) or basal *mucronata* zone Chalk (basal Upper Campanian)	Bawburgh, Norfolk - disused pit near Easton Hall, at road junction immediately SE of Three Corner Plantation	TG 146 096
186, 187, 188, 189	Lower Campanian	restricted *quadrata* zone	Warham, Norfolk, disused pit near Chalk Hill Farm	TF 950 413
201	Lower Campanian	restricted *quadrata* zone, horizon of *Belemnitella praecursor*	Stiffkey Hall Farm Pit, Norfolk	TF 975 428
202	Lower Campanian	restricted *quadrata* zone	Stiffkey, Norfolk, pit by new road beyond Hall Farm	TF 978 435

Table 1.11. Outcrop localities and grid references - Santonian and Coniacian samples.

samples	age	zone	locality	grid reference
16, 17, 18, 19	Coniacian	low *coranguinum* zone	Euston, Suffolk	TL 895 776
113, 114, 115	Coniacian	*coranguinum* zone	South Pickenham, Norfolk	TF 854 042
130, 131, 132, 133, 134, 135	Coniacian or Upper Turonian	basal *coranguinum* zone	Newton by Castle Acre, Norfolk,working Chalk Pit	130 to 133 from N.E. face: TF 837 150; 134, 135 from SE face; TF 837 149
183, 184	Coniacian	*coranguinum* zone	Litcham, Norfolk	TF 888 181, TF 888 178 respectively
14, 15	Santonian	*coranguinum* zone	Stowlangtoft, Suffolk	TL 938 689
47, 48, 49, 50	Santonian	*coranguinum* zone	Helhoughton, Norfolk, quarry	TF 851 273
43	Upper Santonian	*Marsupites* zone	Quidenham, Norfolk	TM 021 872
72	Santonian	*Uintacrinus* zone	Redgrave, Suffolk	TM 056 781
73	Santonian	*Uintacrinus / Marsupites*	Stanton, Suffolk	TL 964 741
148, 149, 150	Santonian or Coniacian	*coranguinum* zone Chalk	Burnham Overy, Norfolk, Rowe's locality 65	TF 843 432
199	Upper Santonian	*Marsupites testudinarius* zone	Houghton St- Giles, near Walsingham, North Norfolk	TF 928 354
2057	Santonian	high *coranguinum* zone	Witham Borehole, Witham, Essex; depth 87.22 -87.45 m	TL 824 41534
2058	Santonian	high *coranguinum* zone	Kelvedon Borehole, Kelvedon, Essex; depth 79.40 - 82.42 m	TL 8602 1797

Fig. 1.9. A diagrammatic section through the Norfolk Chalk (Peake & Hancock, 1961).



Peake & Hancock (1961, fig. 3) present a diagrammatic section through the Norfolk Chalk, correlating this section as it appears in North Norfolk with another from the South of England. This is reproduced as fig. 1.9. In the latter area, the topmost horizon of the Chalk is not known and the section ends at the top of the *Gonioteuthis* Zone.

Peake & Hancock (fig. 6) also present several sections. In the present study, samples were provided by the BGS from Catton Grove (SAG 6-12), Caistor St Edmund (SAG 51-58) and Weybourne (Weybourne Chalk; SAG 61, 60, 59, reproduced in this study as fig. 1.11, annotated to show the position of samples used in the ostracod analysis.

The work on the Upper Chalk of Norfolk was brought up to date with the publication of a further two papers (Peake & Hancock, 2000; Hancock & Peake, 2000). In the former work, the authors note (p. 22) that "when we constructed the zonal map of the Chalk in Norfolk, we were able to visit over 200 sites; today, it would be difficult to find 20." The erosion of the Lower Maastrichtian exposures, as noted in the 1970 addenda and corrigenda has continued over the subsequent thirty years. The huge Mass C of the Grey Beds at Trimingham (Western Mass of Peake and Hancock, 1962, fig. 9, reproduced as fig. 1.13 in this thesis), from which samples SAG 2013 to 2019 were taken, is now "so far seaward of the retreating shoreline as to be completely inaccessible at even the lowest tides helped with offshore winds." A more recent account of the Maastrichtian in Norfolk is that of Whittlesea, 1991.

Fig. 1.10. Catton Grove and Caistor sections (Peake & Hancock, 1961, fig. 6).

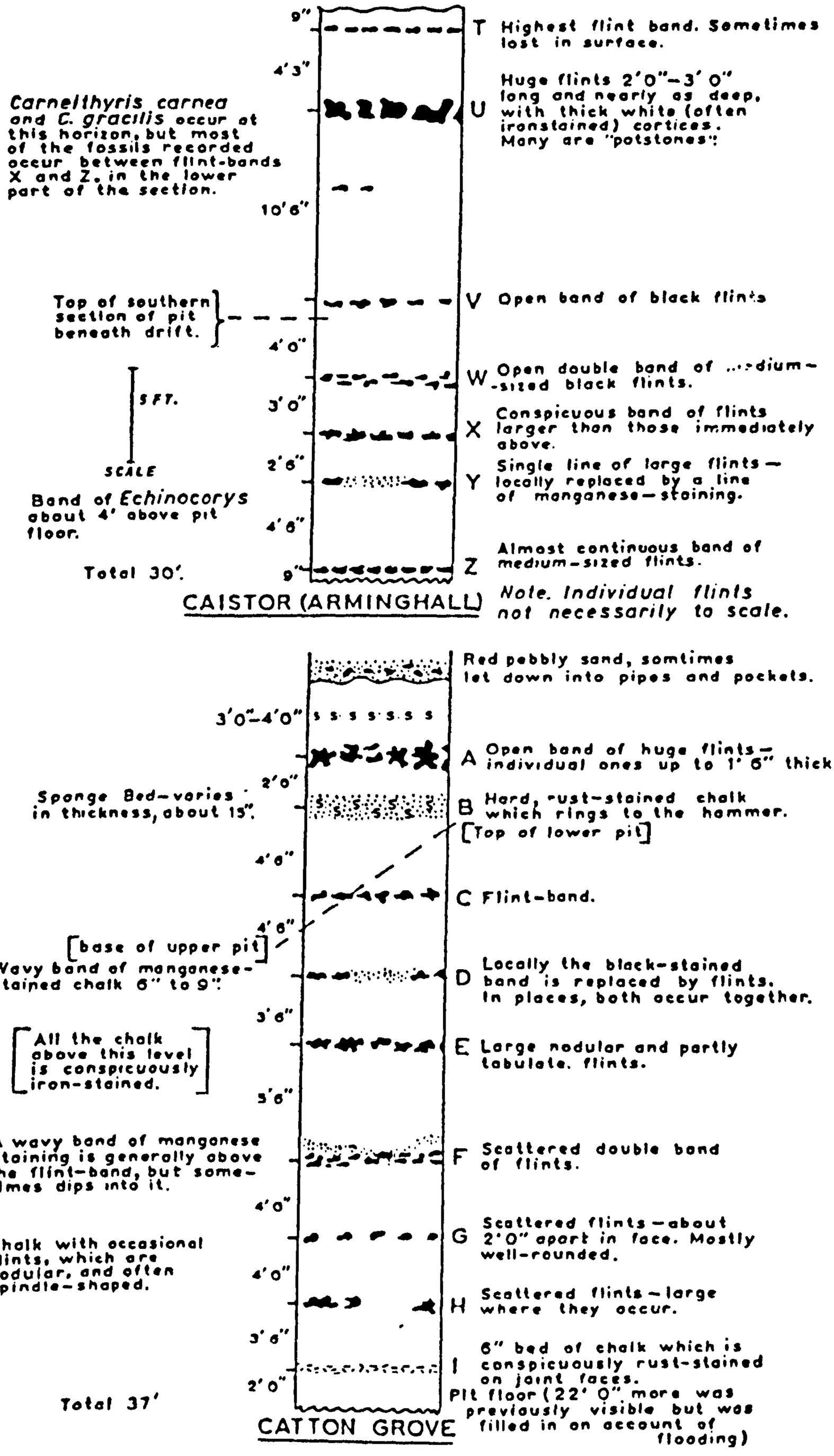


Fig 1.11.Weybourne Chalk section; synthetic vertical section of the Coastal Chalk eastwards from Weybourne Hope (fig. 5 of Peake & Hancock, 1961, p. 315) annotated to show samples from Weybourne, Norfolk.

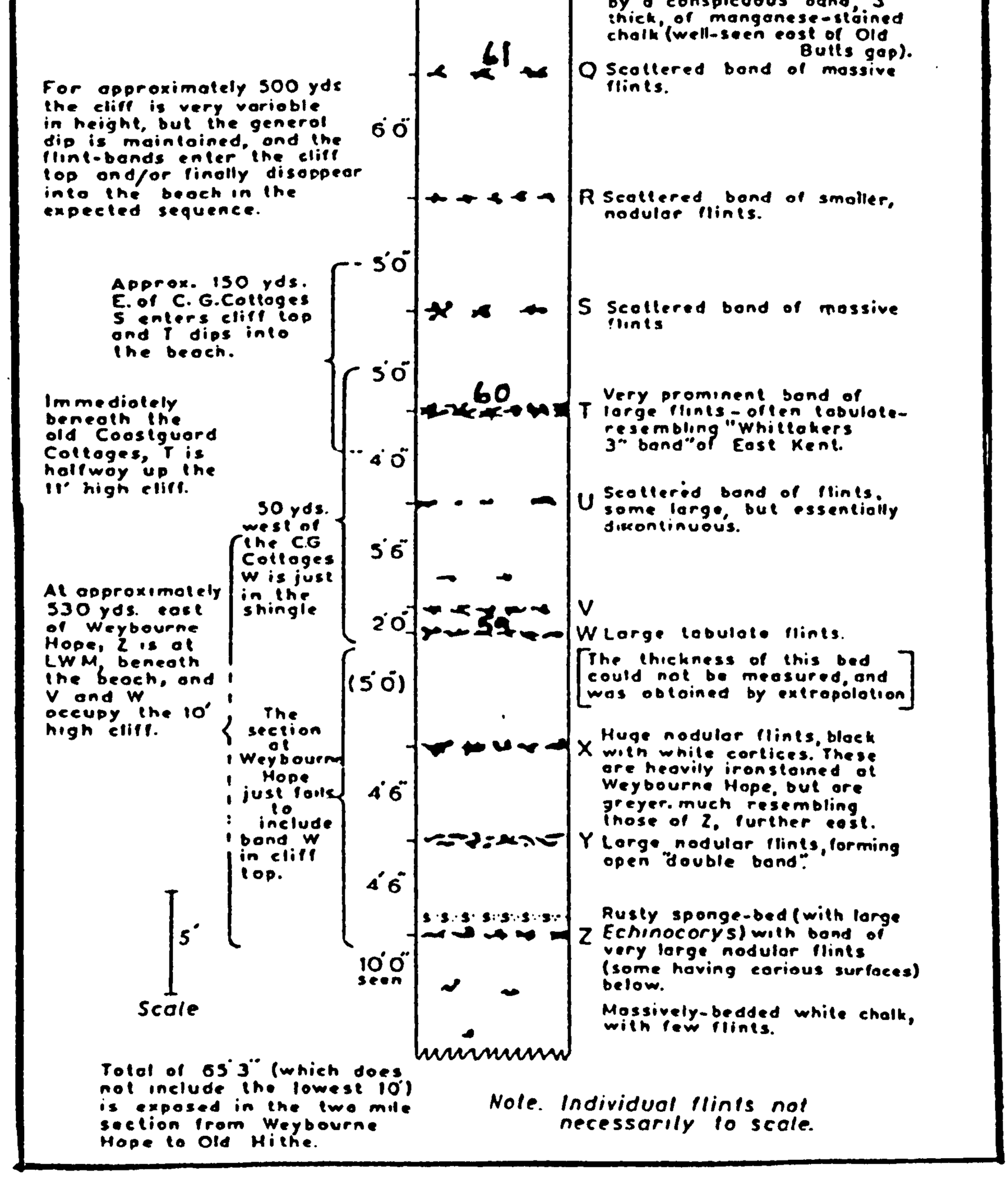
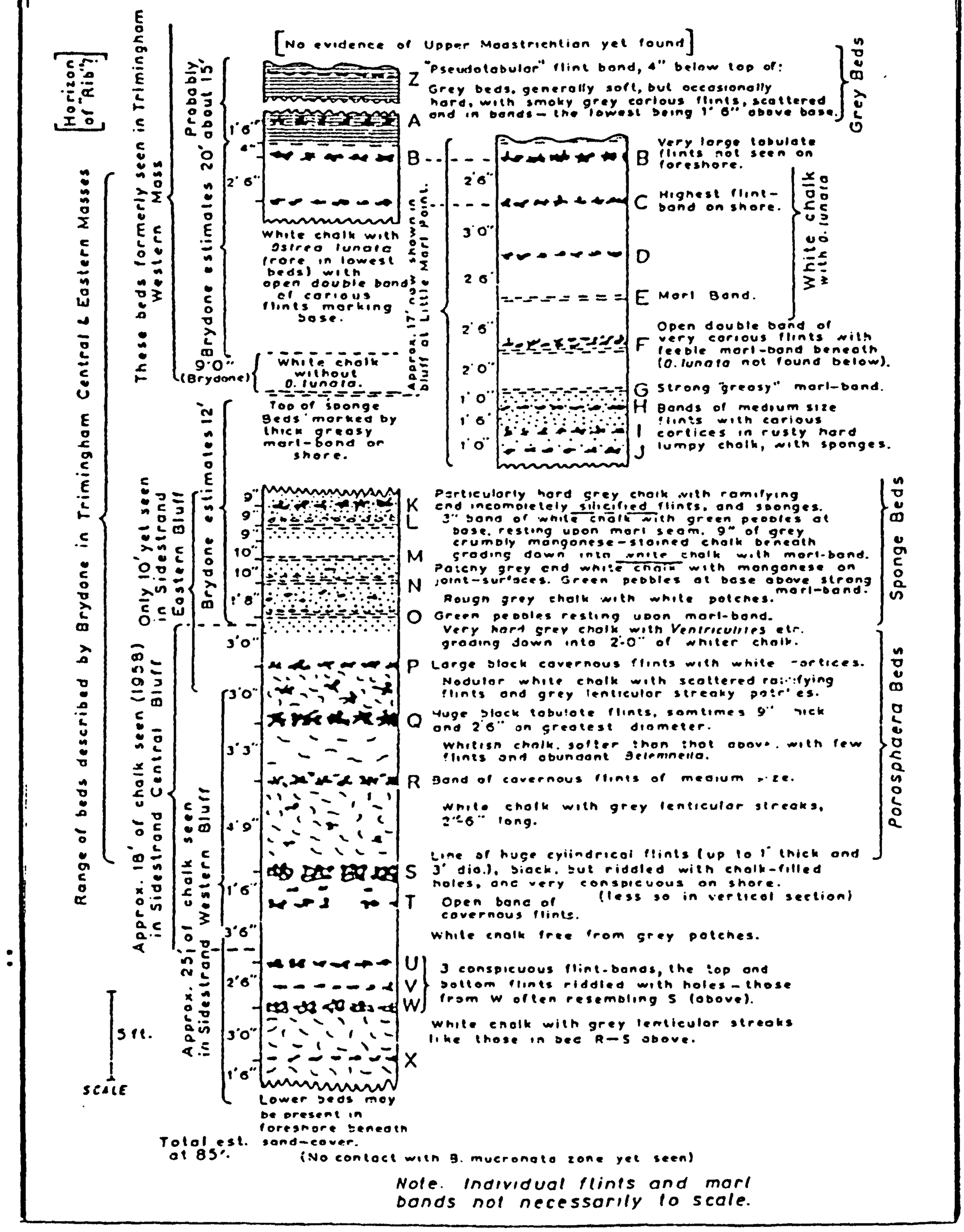


Fig. 1.12. a synthetic vertical section of the Maastrichtian of Sidestrand and Trimingham (Peake & Hancock's fig. 7, p. 322)



Relative relationships of the Lower Maastrichtian samples used in this study:

The various horizons will be discussed in their correct stratigraphical order, from the youngest (Grey Beds) to the oldest (pre-*Porosphaera* Beds).

Grey Beds: (= Beacon Hill Grey member of Johansen & Surluyk, 1990) Four samples in the present study were from the Lower Maastrichtian Grey Beds of Marl Point (reversed dip mass, foreshore exposure) and Little Marl Point, Trimingham, Norfolk. These are as follows: SAG 2006 - between flints A and B, Marl Point; SAG 2007- sample 2, Marl Point; SAG 2008- sample 3, Marl Point; SAG 2010- sample 5, Marl Point;

O. lunata Chalk: There is about thirty feet of white chalk, in the lower nine feet *Ostrea lunata* is extremely rare but, in the remainder, it is abundant. *The O. lunata* Chalk (Johansen & Surlyk, 1990, p. 829 = Little Marl Point Chalk member), therefore, comprises the "White Chalk without *O. lunata*" and the overlying "White Chalk with *O. lunata*" of Peake and Hancock, 1961, 1970, 2000; Hancock & Peake, 2000. It is only known from Northeast Norfolk. In the present study, five samples were taken from the latter horizon; from the overturned foreshore mass at Marl Point, Trimingham.

Fig. 1. 13. Outcrop samples from the O. lunata Chalk

————————	B	flint band
SAG 2004, 2005		white chalk
————————	B1	flint band
SAG 2003		white chalk
————————	C	flint band - highest flint band on shore
SAG 2002		white chalk
————————	D	flint band
SAG 2001		white chalk
- - - - - - - - - -	E	marl band
		white chalk
————————	F	open double band of very carious flints over a feeble marl band, *O. lunata* not found below F

Sponge Beds (=Trimingham Sponge Bed member of Johansen & Surlyk, 1990; see also Wood et al., 1994, p. 105). Peake and Hancock note that "only the top is occasionally exposed at Trimingham, and the lowest few feet are seen at Sidestrand." Consequently, this horizon is poorly represented and was not considered in the present study.

Porosphaera and pre-*Porosphaera* Beds of Sidestrand:

It should be noted at this point that the "Sidestrand Chalk" of Johansen & Surlyk, 1990, (p. 829) encompasses the pre-*Porosphaera* Beds of Wood, 1967 and the "*Porosphaera* Beds" of Brydone, 1906, 1908, 1938. This study uses the earlier terminology.

In the present study, the pre-*Porosphaera* Beds are represented by five samples from the Western Mass (upper monocline) cliff section at Sidestrand, Norfolk. The *Porosphaera* Beds are represented by a further two samples from the same locality.

Fig. 1.14. Outcrop samples from the Porosphaera and pre-Porosphaera Beds

	P	large black cavernous flints with white cortices
		nodular white chalk, scattered ramifying flints, grey lenticular streaky patches
	Q	huge black tabulate flints
SAG 2019		whitish chalk, softer than above, with few flints and abundant *Belemnella*
	R	band of cavernous flint of medium size
SAG 2018		white chalk with grey lenticular streaks
	S	line of huge cylindrical flints
SAG 2017		
	T	open band of cavernous flints
SAG 2016		white chalk, free from grey patches
	U	flint bands U, V and W conspicuous
SAG 2015, 2014		
	V	
SAG 2013		
	W	white chalk with grey lenticular streaks, like those of bed R-S

Peake and Hancock (1961, p. 321) describe the beds as being composed of soft, but massive, chalk with flint bands - two of which are very distinctive, "especially where exposed upon bedding planes in the beach platform, where the 'flints with holes' stand proud like huge sultana cakes.". Some of the chalk also contains irregularly orientated blueish grey lenticular streaks which are on average about six inches long.

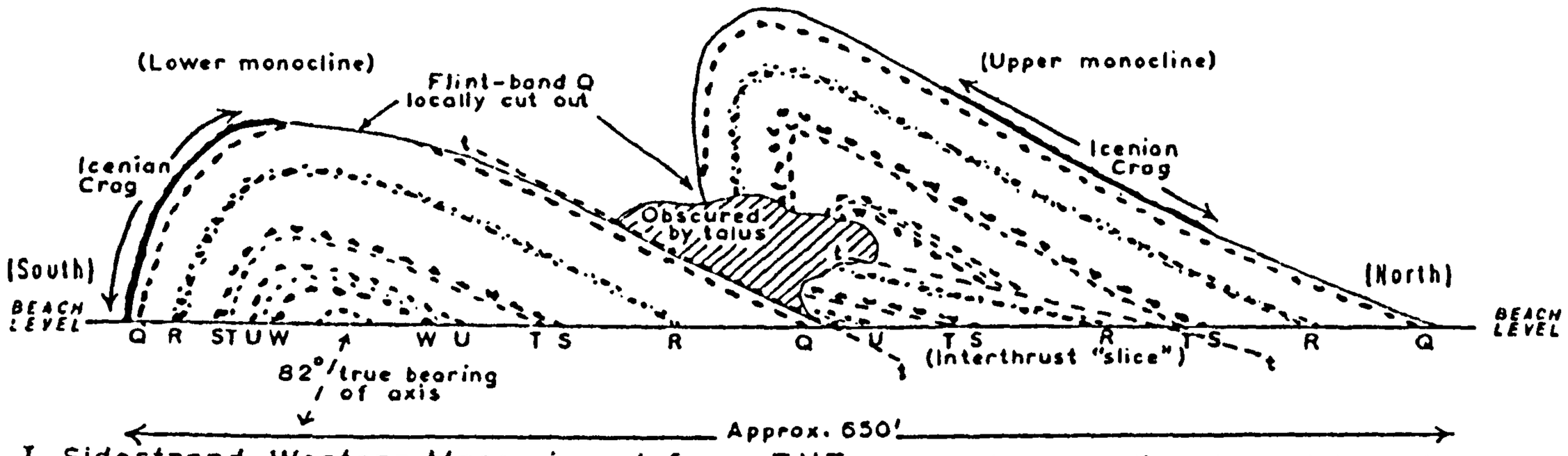
The effects of the Pleistocene glaciation on the Chalk in Norfolk

The Chalk of Northern Norfolk has been affected by Pleistocene ice movements. Peake & Hancock (pp. 324, 325, fig. 8, reproduced as fig. 1.15 of this thesis) extensively discuss this, stating that "scattered over the north and east of the country are many erratic blocks, in some of which the bedding is virtually undisturbed while in others, the matrix is extensively rearranged, with the flints shattered and drawn out in stringers; some show even more complete rearrangement - the chalk having lost all trace of its original structure, and incuding waterworn pebbles of flint and other rocks, together with derived fossils of all ages up to Pleistocene. This last type must be regarded as Pleistocene deposits made up of predominantly material from the Cretaceous beds over which the ice passed.... Erratic blocks of similar material are seen at Weybourne and Beeston, and at several points high in the cliffs between the latter place and Mundesley. No stratigraphical consideration can be given to these, nor to the inland erratics, since their field relationships can seldom be made out."

There are, however, several masses of chalk along the coast between Sheringham and Mundesley which "are (or have been) well enough exposed to contribute usefully to our stratigraphical knowledge." An example of such a series of chalk masses occurs at Overstrand. The first exposure here was noted in 1878 and Brydone, in 1906, states that by 1896 there were no less than ten of these masses. Artificial sloping had obscured them by 1905, but erosion since 1939 has once again exposed the eastern and largest, beneath the site of the Overstrand hotel. In the present study, this locality is represented by SAG 1, 2 and 4. The assemblage data for these three samples is included in a separate discussion in the appendix 2, since they were studied at a late stage in this research and do not figure in the main body of the thesis or in the biostratigraphical range charts drawn for the Lower Maastrichtian. According to Peake & Hancock (p. 325), the chalk mass at Overstrand is about 300 feet long, and its western end appears to exhibit a 40 foot vertical section of chalk dipping at 15 degrees south, consisting of a series of overthrust repetitions of the same set of beds. The uppermost bed is the most complete and comprises 15 feet of "hardish" white chalk with seven bands of medium sized flints. The planes of separation appear as marl bands in the face of the bluff. Specimens of *Belemnitella mucronata* have been found here, apparently representing the the highest *B. mucronata* zone Chalk exposed in Norfolk.

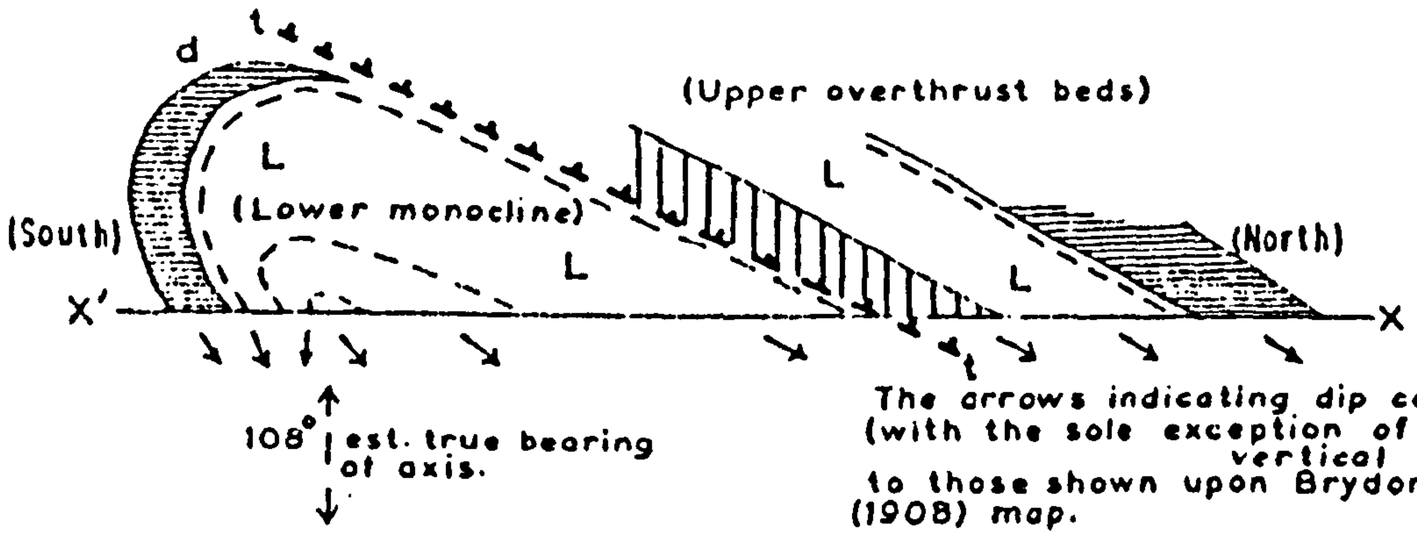
In 1937, Brydone reported the appearance of a mass of chalk in the cliff at Sidestrand and, by 1948, this had the form shown in Peake & Hancock's figure 8i. This is reproduced in this thesis as figure 1.15.

Fig. 1.15. Glacially moved masses near Sidestrand and Trimingham overthrust towards the South (from Peake & Hancock, 1961, fig. 8, p. 327)

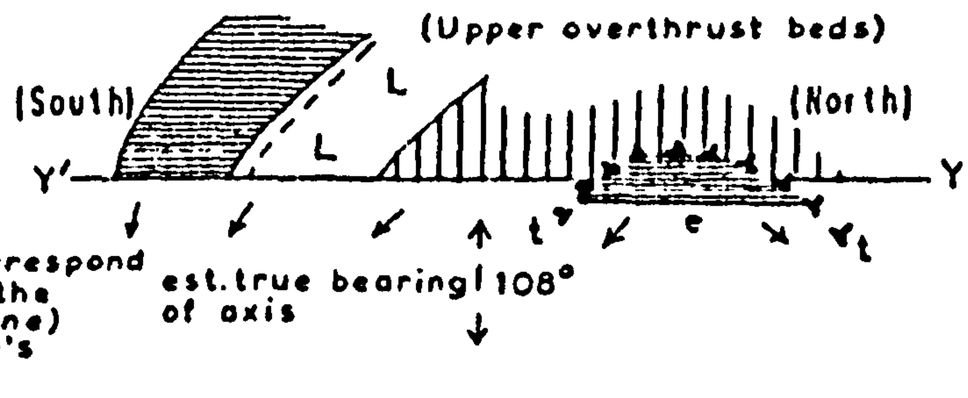


I Sidestrand Western Mass viewed from ENE ie. looking along core of monocline from shore. (reproduced from actual photograph)

Note. Diagrammatic only—not to scale. Pleistocene beds omitted. Letters refer to actual flint-bands as indicated in vertical section.



II A. Section along X–X', viewed from east.



II B. Section along Y–Y', viewed from east. The grey beds 'e' are a continuation of 'd' (on fig. II A) and appear as a tectonic window viewed through the eroded bed of the upper series.

II Hypothetical reconstruction of the Trimingham Western Mass before recent marine peneplanation. The scale is greater than that of the map of the foreshore exposures, but the symbols used are the same.

Fig. 1.16 The foreshore exposure near Trimingham (Peake & Hancock, 1961, fig. 9)

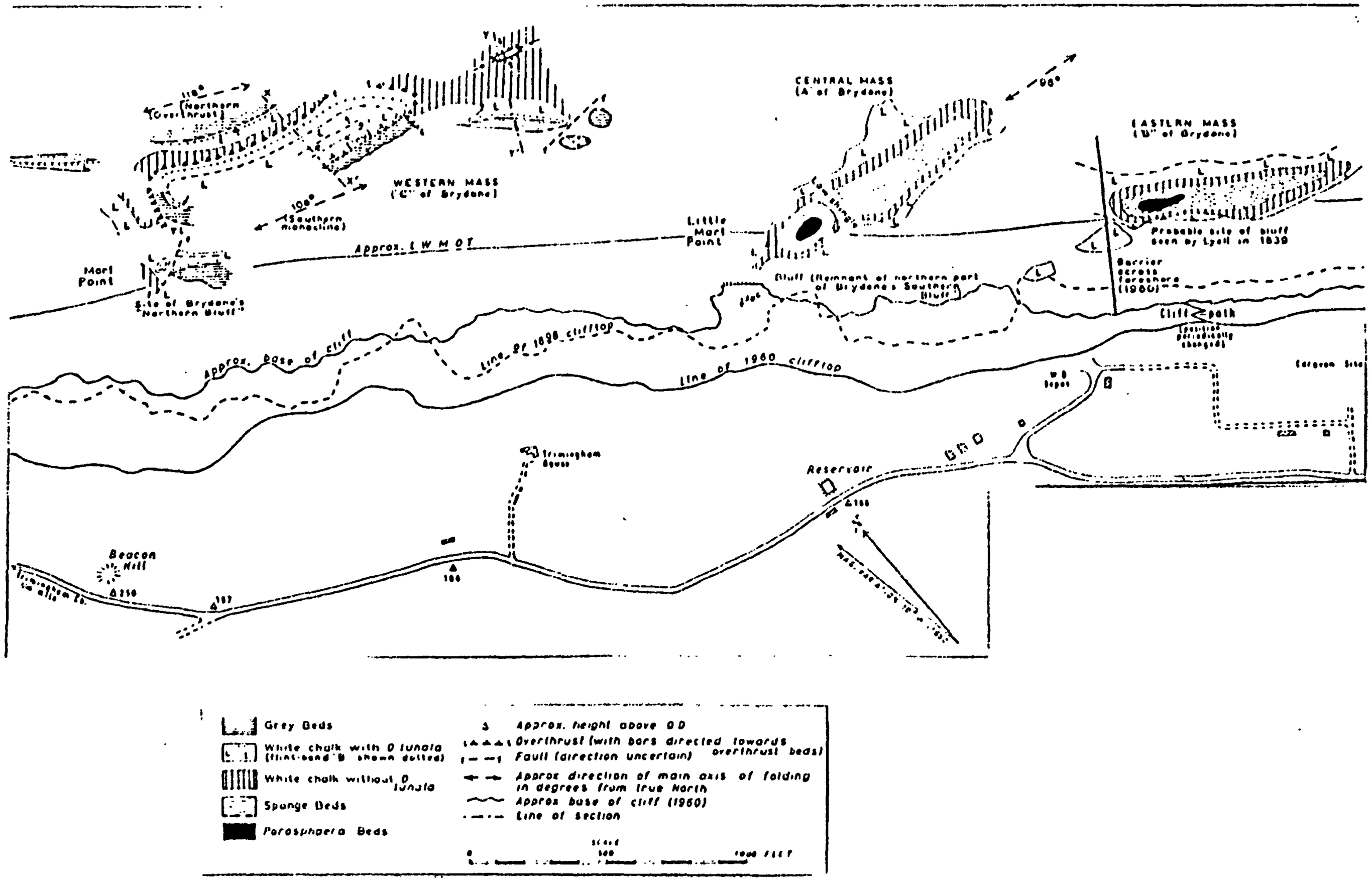
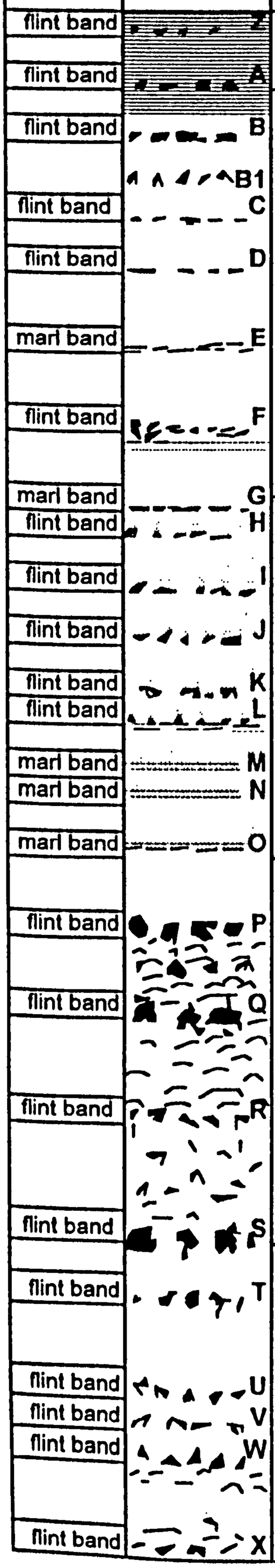
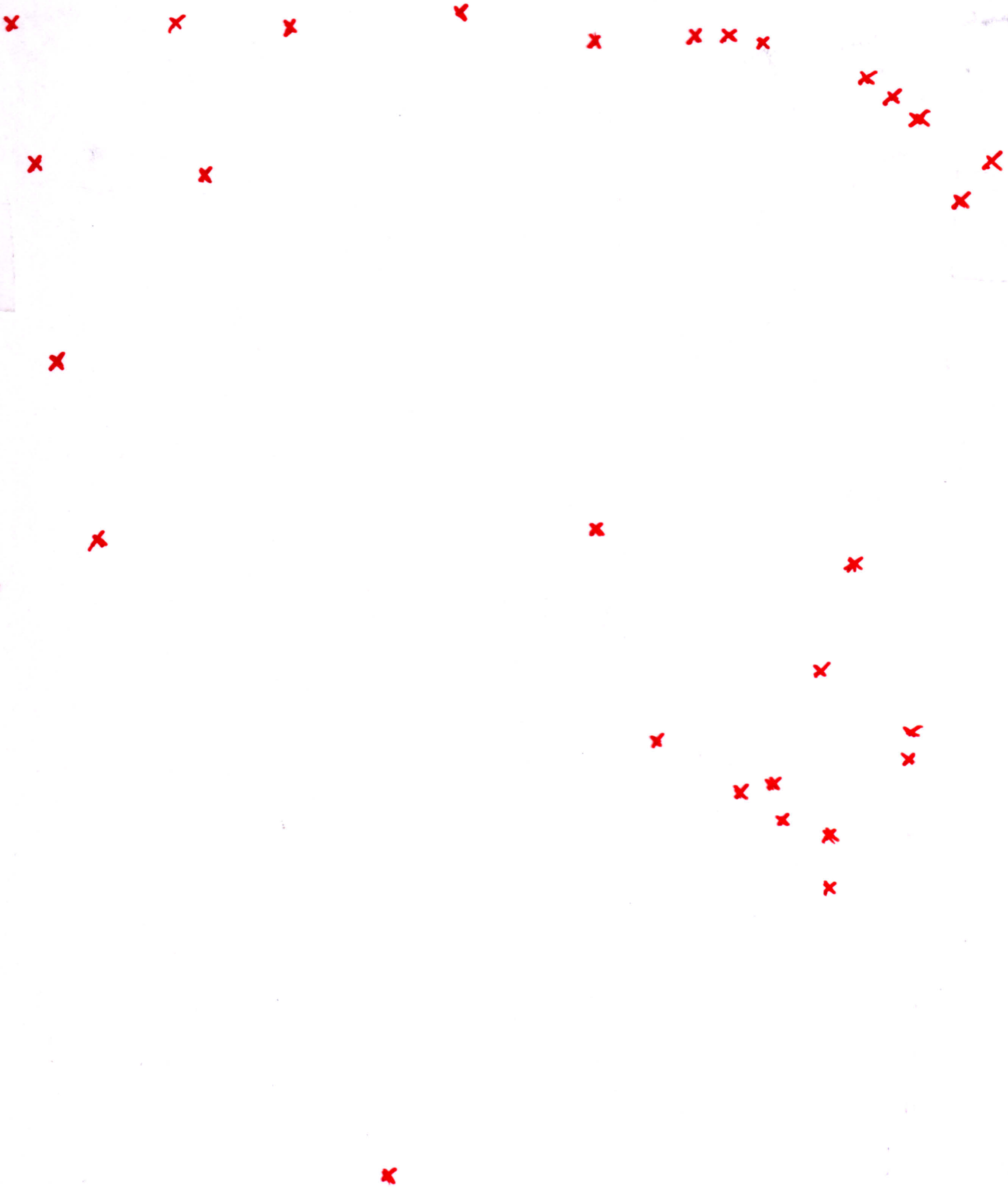


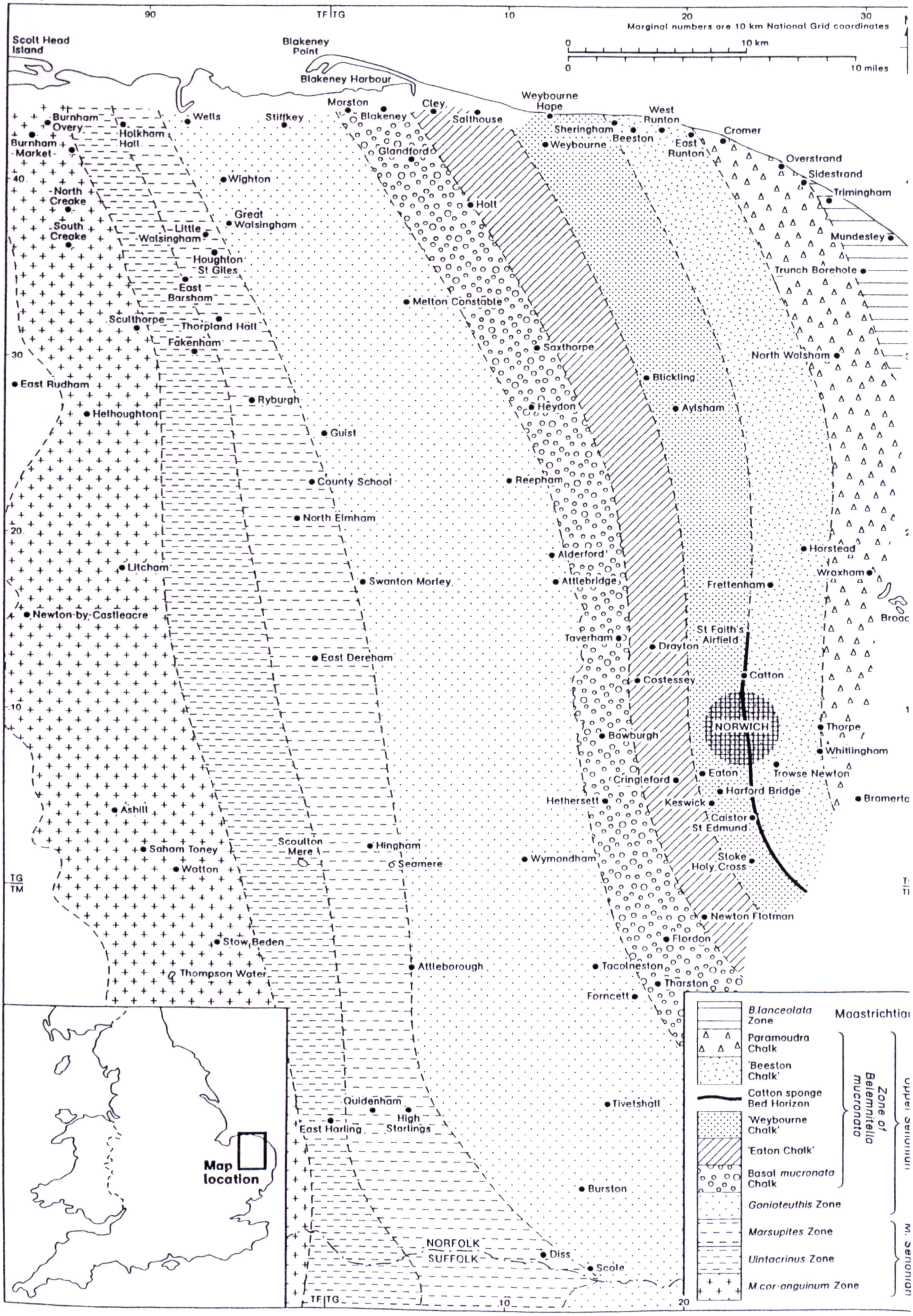
Fig. 1.17 Suggested stratigraphical relationships of the Lower Maastrichtian Trunch Borehole samples with the outcrop samples from Sidestrand and Trimingham

A schematic vertical section based on Peake and Hancock (1961, p. 322, fig. 7), annotated to include recent work by such authors as Johansen & Surlyk, 1990; Wood et al., 1994; Peake and Hancock, 2000 and Hancock & Peake, 2000. Reference was made to the BGS stratigraphical log for the Trunch Borehole (appendix 3). The Sponge Beds are poorly represented at Trimingham, which explains the hiatus in samples between the *O. lunata* Chalk and the *Porosphaera* Beds



Flint band	Trunch Borehole	outcrop	subdivision according to Peake & Hancock (1961, 1970, (2000; Hancock & Peake, 2000	equivalent members (Johansen & Surlyk, 1990)
flint band A flint band	not studied	SAG 2010 SAG 2008 2007, 2006	Grey Beds	Beacon Hill Grey Chalk
flint band B B1 flint band C flint band D marl band E flint band F	not studied	SAG 2005 SAG 2004 SAG 2003 SAG 2002 SAG 2001	White Chalk with O. lunata	Little Marl Point Chalk
marl band G	not studied	not studied	White Chalk without *O. lunata*	
flint band H flint band I flint band J flint band K flint band L marl band M marl band N marl band O	not studied	not studied	Sponge Beds	Trimingham Sponge Beds
flint band P flint band Q flint band R flint band S	SAG 213 SAG 216 SAG 217	SAG 2019 SAG 2018	*Porosphaera* Beds	Sidestrand Chalk
flint band T flint band U flint band V flint band W flint band X	SAG 221 SAG 231	SAG 2017 SAG 2016 SAG 2015, 2014 SAG 2013	pre - *Porosphaera* Beds	




90
TF | TG
10
20
30
Marginal numbers are 10 km National Grid coordinates
0
10 km
0
10 miles
Scolt Head Island
Blakeney Point
Blakeney Harbour
Morston
Blakeney
Cley
Salthouse
Weybourne Hope
West Runton
Cromer
Overstrand
Sidestrand
Trimingham
Mundesley
Trunch Borehole
North Walsham
Horstead
Wroxham
Broac
Sheringham
Beeston
East Runton
Weybourne
Glandford
Holt
Melton Constable
Saxthorpe
Blickling
Aylsham
Heydon
Reepham
Alderford
Attlebridge
Frettenham
Taverham
Drayton
Costessey
Bawburgh
NORWICH
Cringleford
Eaton
Hethersett
Keswick
Harford Bridge
Caistor St Edmund
Stoke Holy Cross
Wymondham
Newton Flotman
Flordon
Tacolneston
Tharston
Forncett
Tivetshall
Burston
Diss
Scole
Thorpe
Whitlingham
Trowse Newton
Bramerto
St Faith's Airfield
Catton
Wells
Stiffkey
Burnham Overy
Holkham Hall
Burnham Market
Wighton
North Creake
South Creake
Great Walsingham
Little Walsingham
Houghton St Giles
East Barsham
Sculthorpe
Thorpland Hall
Fakenham
East Rudham
Ryburgh
Helhoughton
Guist
County School
North Elmham
Litcham
Swanton Morley
Newton-by-Castleacre
East Dereham
Ashill
Saham Toney
Watton
Scoulton Mere
Hingham
Seamere
Stow Bedon
Attleborough
Thompson Water
Quidenham
East Harling
High Starlings
NORFOLK
SUFFOLK
Map location
TG
TM
B.lanceolata Zone
Paramoudra Chalk
'Beeston Chalk'
Catton sponge Bed Horizon
'Weybourne Chalk'
'Eaton Chalk'
Basal mucronata Chalk
Gonioteuthis Zone
Marsupites Zone
Uintacrinus Zone
M.cor-anguinum Zone
Zone of Belemnitella mucronata
Maastrichtian
Upper Senonian
M. Senonian

90 TF | TG 10 20 30

Marginal numbers are 10 km National Grid coordinates

0 10 km

0 10 miles

Scolt Head Island

Blakeney Point

Blakeney Harbour

Morston

Blakeney

Cley

Salthouse

Weybourne Hope

Sheringham

Weybourne

West Runton

Beeston

East Runton

Cromer

Overstrand

Sidestrand

Trimingham

Mundesley

Trunch Borehole

North Walsham

Horstead

Wroxham

Broac

Frettenham

Aylsham

Blickling

Heydon

Reepham

Alderford

Attlebridge

Taverham

Drayton

Costessey

St Faith's Airfield

Catton

NORWICH

Thorpe

Whitlingham

Trowse Newton

Eaton

Cringleford

Harford Bridge

Bramerto

Hethersett

Keswick

Caistor St Edmund

Wymondham

Stoke Holy Cross

Newton Flotman

Flordon

Tacolneston

Tharston

Forncett

Tivetshall

Burston

Diss

Scole

Wighton

Great Walsingham

Little Walsingham

Houghton St Giles

East Barsham

Thorpland Hall

Fakenham

Ryburgh

Guist

County School

North Elmham

East Dereham

Hingham

Seamere

Scoulton Mere

Thompson Water

Attleborough

Stow Bedon

Saham Toney

Watton

Ashill

Swanton Morley

Litcham

Newton-by-Castleacre

Helhoughton

East Rudham

Melton Constable

Saxthorpe

Glandford

Holt

Stiffkey

Wells

Burnham Overy

Holkham Hall

Burnham Market

North Creake

South Creake

Quidenham

East Harling

High Starlings

NORFOLK

SUFFOLK

Map location

	B.lanceolata Zone
	Paramoudra Chalk
	'Beeston Chalk'
	Catton sponge Bed Horizon
	'Weybourne Chalk'
	'Eaton Chalk'
	Basal *mucronata* Chalk
	Gonioteuthis Zone
	Marsupites Zone
	Uintacrinus Zone
	M.cor-anguinum Zone

Maastrichtian

Upper Senonian

Zone of Belemnitella mucronata

M. Senonian

European Upper Cretaceous Ostracod faunas compared and contrasted with those of East Anglia.

1) FRANCE. The French Senonian is characterised by its great richness in ostracods in both the Northern Realm (e. g. Paris Basin - Damotte, 1963, 1964, 1965, 1971a, 1971b) and the Tethyan Realm (e. g. Provence - Babinot, 1980; Babinot & Tronchetti, 1983; Babinot *et al.*, 1983). The Tethyan Realm is divided into four main palaeobiogeographical units: South European, North-central America, Afro-Arabian and Austral bioprovinces. The Tethyan faunas of Provence fall into the first of these divisions.

In Provence, biozonation of the Coniacian to Santonian has been established by means of planktonic foraminifera. Ostracods have been integrated into this framework. Babinot & Colin (1992) examined marine ostracod provincialism in the Late Cretaceous of the Tethyan Realm. "Many authors have pointed out that, because of taxonomic inconsistencies, genera are more reliable than species for a clear definition of bioprovinces.". Such bioprovinces often show a strong endemism at specific level, moderated by the existence of a few ubiquitous genera (for example *Cytherella*, *Cytherelloidea, Bairdia* (=*Bairdopillata).* A synthesis of the palaeobiogeography of Tethyan ostracod faunas for the entire Cretaceous was published by the same authors in 1988. Several factors are responsible for palaeobiogeographical distributions and provincialism and their evolution: the position and extension of continental margins, oceanic surface current patterns, palaeobathymetry, eustatic sea level changes and palaeolatitude. Other parameters are the biology, physiology and ecology of the ostracods themselves (Babinot & Colin, 1992, p. 283; Babinot *et al.*, 1985, Benson, 1988, Whatley, 1988).

Genera recorded in previous studies - The Northern Realm -

1) Paris Basin (Damotte, 1971a)

Genera present are as follows:

Amphicytherura Butler & Jones, 1957,

Asciocythere Swain, 1952,

Aversovalva Hornibrook, 1952,

Bairdia (= *Bairdoppilata* Coryell, Sample & Jennings, 1935),

Bythoceratina Hornibrook, 1952,

Centrocythere Mertens, 1956 (= a subgenus of *Neocythere)*

Curfsina Deroo, 1966,

Cythereis Jones, 1849 (includes all those later put into *Hazelina, Oertliella, Limburgina, Rehacythereis)* by subsequent authors),

Cytherella Jones, 1849,

Cytherelloidea Alexander, 1929,

Dumontina Deroo, 1966,

Isocythereis Triebel, 1958,

Karsteneis Pokorny, 1963,

Krithe Brady, Crosskey & Robertson, 1847,

Monoceratina Roth, 1928,

Mosaeleberis Deroo, 1966,

Neocythere (Neocythere) Mertens, 1956,

Neocythere (Physocythere), Kaye, 1964,

Occultocythereis Howe, 1951,

Paracypris Sars, 1866,

Phacorhabdotus Howe & Laurencich, 1958,

Platycythereis Triebel, 1940,

Pterygocythereis (Pterygocythere) Hill, 1954 = *Pterygocythere* in present study,

Pterygocythereis (Pterygocythereis) Blake, 1933 = *Pterygocythereis* in present study,

Spinoleberis Deroo, 1966,

Trachyleberidea Bowen, 1953,

Xestoleberis Sars, 1866.

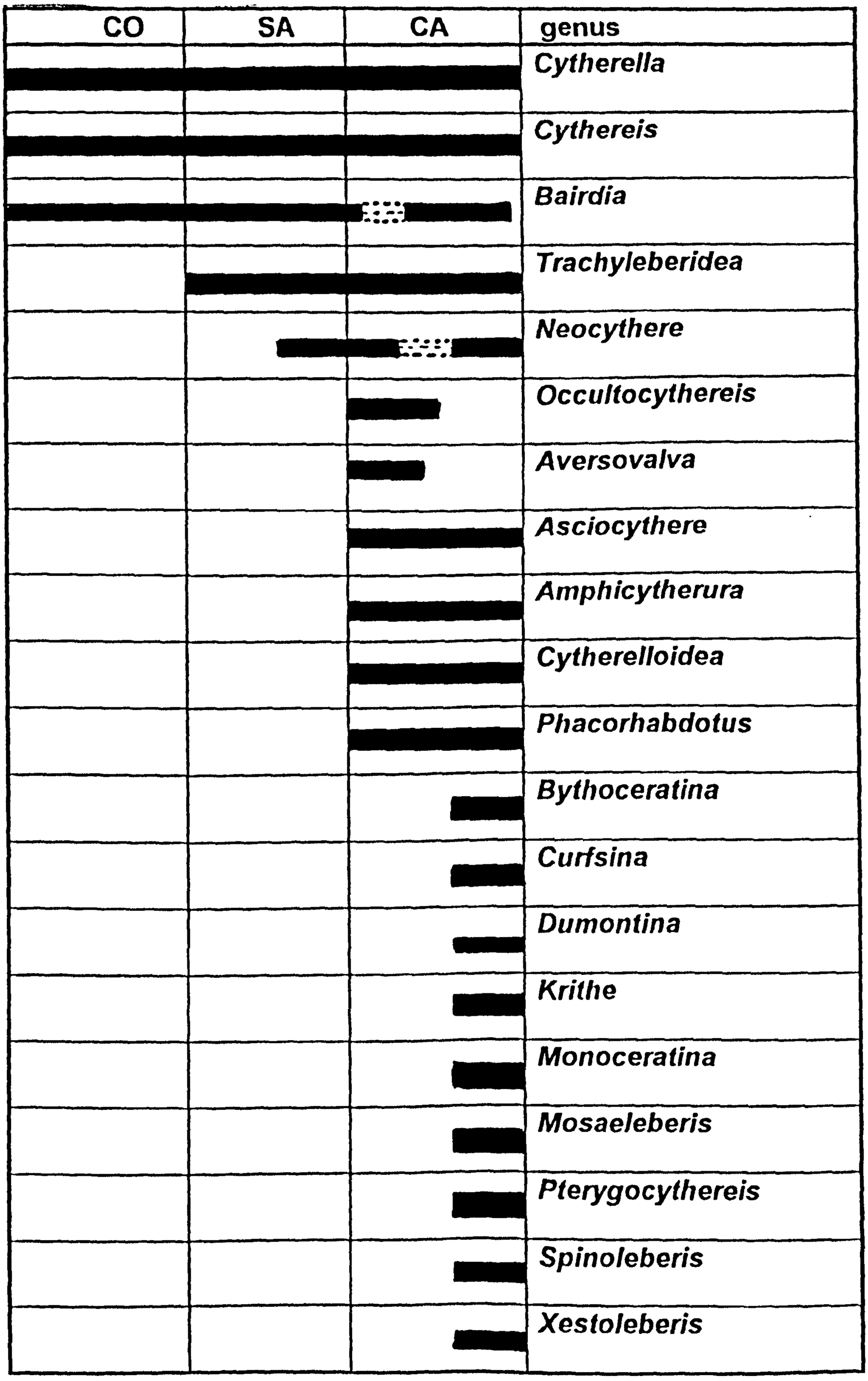
Number of genera present = 27

Number of genera also recorded in this study = 21

The present author has analysed all the genera present in Damotte's 1971a study of the Paris Basin and produced a stratigraphical range chart for 20 genera across the Coniacian to Lower Maastrichtian. This is included in the thesis as figure 1.20.

The fauna, especially when considered at generic level, is similar to that seen in the material from the Trunch Borehole and various outcrop localities in Norfolk and Suffolk. Most genera seen in the Paris Basin are also represented in East Anglia, with the exeption of *Dumontina*, *Isocythereis*, *Karsteneis* and *Occultocythereis.* Species which occur in both areas include *Cytherella ovata, Cytherella parallela, Cytherelloidea hindei, Cytherelloidea granulosa, Bairdoppilata septentrionalis, Phacorhabdotus lonsdaleiana, Phacorhabdotus semiplicatus, Cythereis longaeva longaeva, Limburgina cf. senonensis, Mosaeleberis macropthalma, Trachyleberidea acutiloba, Bythoceratina umbonatoides, Monoceratina pedata pedata, Neocythere virginea* and others. The faunas of Britain are closer to those of the Northern Realm (Northern France) than they are to the Tethyan Realm (Southern France - Provence and Aquitaine). Guignot (1955, p. 421) notes that in Britain "the Upper Cretaceous here is quite analogous to that of the Paris Basin."

Fig. 1.20. Damotte, 1971a - Paris Basin



2) Paris Basin (Babinot, Colin & Damotte, 1983) The following genera are encountered in this study:

Amphicytherura Butler & Jones, 1957,
Asciocythere Swain, 1952,
Aversovalva Hornibrook, 1952,
Bairdia (=Bairdoppilata Coryell, Samlple & Jennings, 1935),
Bythoceratina Hornibrook, 1952,
Cuneoceratina Gründel & Kozur, 1971,
Curfsina Deroo, 1966,
Cytherella Jones, 1849,
Cytherelloidea Alexander, 1929,
Cythereis Jones, 1849,
Dolocytheridea Triebel, 1938,
Dumontina Deroo, 1966,
Imhotepia Gründel, 1969,
Kamajcythereis Pokorny & Colin, 1976,
Karsteneis, Pokorny, 1963,
Krithe Brady, Crosskey & Robertson, 1847,
Limburgina Deroo, 1966,
Mauritsina Deroo, 1962,
Mosaeleberis Deroo, 1966,
Neocythere Mertens, 1956,
Occultocythereis Howe, 1951,
Oertliella Pokornky, 1964,
Paracypris Sars, 1866,
Parapokornyella Babinot, 1980 MS,
Phacorhabdotus Howe & Laurencich, 1958,
Pterygocythere Hill, 1954,
Pterygocythereis Blake, 1933,
Spinoleberis Deroo, 1966,
Trachyleberidea Bowen, 1953.

Number of genera =29 Number of genera which also appear in the present study = 22.

The present author has analysed all the genera listed by Babinot *et al.*, in their study of the Paris Basin, and has produced a stratigraphical range chart (fig. 1.21). The ranges quoted by Damotte are compared with those given by the former authors in fig.1.22. The faunas, when considered at generic level are similar to Damotte's ranges, but less comparable with the assemblages in East Anglia. Most genera listed in the 1983 study, however, are also present in the current study, with the exception of *Dumontina, Karsteneis, Occultoocythereis, Kamajcythereis, Dolocytheridea, Imhotepia and Parapokornyella.*

Fig. 1.21. Babinot et al., 1983 - Paris Basin

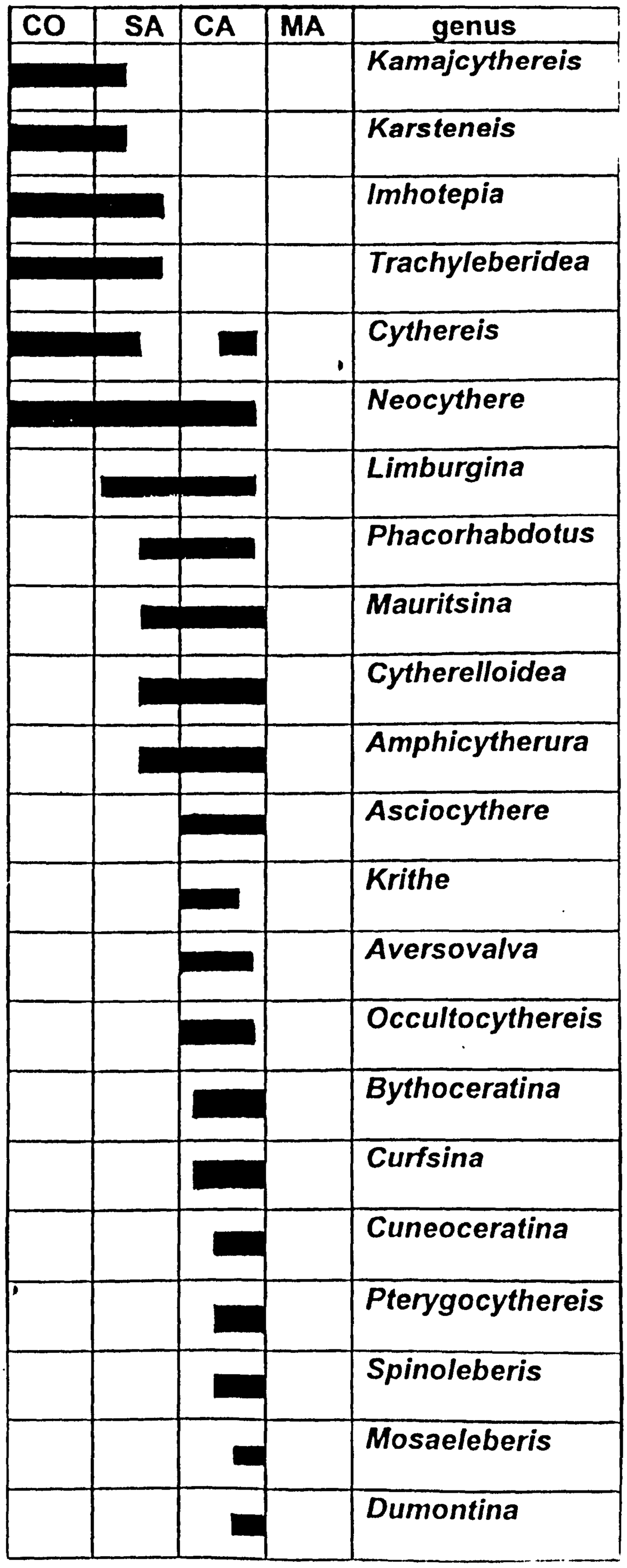


Fig. 1.22. Generic ranges of selected genera in the Paris Basin.

This figure brings together the ranges of both Damotte (1971a) ~~~~~~~~~~ and Babinot et al., (1983) ++++++++++, enabling comparisons to be made between the generic ranges given in the two publications.

CO	SA	CA	genus
~~	~~~~~~~~~	~~~~~~~~~~	*Cytherella*
~~ ++++++++++	~~~~~~~~~~ ++++	~~~~~~~~~~ ++++	*Cythereis*
~~	~~~~~~~~~	~~~~~	*Bairdia*
++++++++++	~~~~~~~~~~ +++++++	~~~~~~~~~~	*Trachyleberidea*
++++++++++	~~~~~ ++++++++++	~~~ ~~~ ++++++++	*Neocythere*
		~~ ++++++++	*Occultocythereis*
		~~ ++++++++	*Aversovalva*
		~~ ++++++++	*Asciocythere*
	++++++	~~~~~~~~~ ++++++++++	*Amphicytherura*
		~~ ++++++++	*Cytherelloidea*
		~~ ++++++++	*Phacorhabdotus*
		~~ ++++++++	*Bythoceratina*
		~~ ++++++++	*Curfsina*
		~~ +++	*Dumontina*
		~~ +++++	*Krithe*
		~~ ++++	*Mosaeleberis*
		~~ ++++	*Pterygocythereis*
		~~ +++++	*Spinoleberis*
		~~	*Xestoleberis*

2) Genera recorded in previous studies - the Tethyan Realm i) Babinot, 1980 - Provence:

The following genera were recorded in this study:

Bairdia (= Bairdoppilata Coryell, Sample & Jennings, 1935,
Bythocypris Brady, 1880,
Bythoceratina Hornibrook, 1952,
Chapmanicythereis Gründel, 1973 (=junior synonym of *Platycythereis*),
Costaveenia Gründel, 1968,
Cuneoceratina Gründel & Kozur, 1971,
Curfsina Deroo, 1966,
Cytherella Jones, 1849,
Cytherelloidea Alexander, 1933,
Dolocythere Mertens, 1956,
Dolocytheridea Triebel, 1938,
Dordionella Apostolescu, 1955,
Eucytherura Müller, 1894,
Hazelina Moos, 1966,
Horrificiella Liebau, 1975,
indet. gen. 1 (pl. 52, fig. 5),
indet. gen. 4 (pl. 53, figs 1-4),
indet. gen. 6 (pl. 53, fig. 5),
indet. gen. 7 (pl. 53, figs 6, 7),
indet. gen. 9 (pl. 53, figs 10-14),
Kalyptovalva Howe & Laurencich, 1958,
Karsteneis Pokorny, 1963,
Kingmaina Keij, 1957,
Limburgina Deroo, 1966,
Mauritsina Deroo, 1962,
Mosaeleberis Deroo, 1966,
Neocythere (Physocythere) Mertens, 1956,
Occultocythereis Howe, 1951,
Oertliella Pokorny, 1964,
Paracaudites (*Dumontina*) Deroo, 1966,
Paracyprideis (Mutacyprideis) Klie, 1929,
Paracypris Sars, 1866,
Parakrithe Van den Bold, 1958,
Parapokornyella Babinot, 1980,
Planileberis Deroo, 1966,

Posacythere nov. gen.,
Pterygocythere Hill, 1954,
Pterygocythereis Blake, 1933,
Risaltina Colin & Grekoff, 1973,
Schuleridea Swartz & Swain, 1946,
Spinoleberis Deroo, 1966,
Trachyleberidea Bowen, 1953,
Uroleberis Triebel, 1958,
Valdoniella nov. gen.,
Veeniaceratina Gründel & Kozur, 1972
Xestoleberis Sars, 1866.

Number of genera (not including indet. gen.) = 41
Number of genera also represented in the present study = 20.

The present author has analysed all the genera listed in Babinot's 1980 study of the ostracods of Provence, and produced a stratigraphical range chart (fig. 1. 23). The fauna is different from the Northern Realm fauna of the Paris Basin and contains more elements that are not represented in the Upper Chalk of East Anglia (Trunch Borehole or outcrop samples). In many cases, they do not occur in any published British record). Of the 41 genera, less than half are seen in the present study. Absent genera include *Costaveenia, Dolocythere, Dolocytheridea, Dordionella, Hazelina, Kalyptovalva, Karsteneis, Kingmaina, Occultocythereis, Paracaudites, Paracyprideis, Uroleberis, Parapokornyella* and others. These genera may characterise a typically warmer water Southern European fauna of the Tethyan Realm as they are also less common or absent in the faunas of Northern Europe (e. g. Germany, Netherlands, Belgium).

Species which do occur in both the present thesis and in Babinot's 1980 study include *Cytherella ovata, Cytherella parallela, Bairdoppilata septentrionalis, Monoceratina pedata pedata, Trachyleberidea acutiloba, Limburgina senonensis, Eucytherura dorsotuberculata*. These species appear more ubiquitous, with no apparent biogeographical preferences.

It should be noted that both Babinot, 1980 and Babinot *et al.*, 1983, detail a marine and a freshwater component (the latter being characterised by genera such a *Valdoniella, Candona, Paracandona, Ilyocypris, Darwinula).* The assemblages of East Anglia are exclusively marine, as are those of the Northern Realm (Paris Basin).

The range chart (figure 1. 23) drawn using Babinot's generic ranges only extends, therefore, from the Coniacian to the Upper Santonian. In the Campanian, marine faunas give way to a freshwater fauna. The range chart deals mainly with the marine component and some freshwater forms have been omitted.

Fig. 1.23. : Babinot, 1980, Provence

CO	lower SA	middle SA	upper SA	genus
				Bairdia
				Curfsina
				Cytherella
				Dolocytheridea
				Dordionella
				Limburgina
				Mauritsina
				Paracaudites
	---?---			*Parakrithe*
				Parapokornyella
				Trachyleberidea
		?		*Pterygocythere*
				Kalyptovalva
				Bythocypris
				Kingmaina
				Costaveenia
				Planileberis
				Mosaeleberis
				Spinoleberis
				Chapmanicythereis

Fig. 1.23. Babinot, 1980 - Provence (continued).

CO	lower SA	middle SA	upper SA	genus
				Cytherelloidea
				Horrificiella
				Karsteneis
				Schuleridea
				Uroleberis
				Xestoleberis
				Bythoceratina
				Neocythere
				Occultocythereis
				Oertliella
				Paracyprideis
				Pterygocythereis
				Veeniaceratina
				*Cuneoceratina***
				*Eucytherura***
				*Hazelina***
				*Paracaudites?***
				*Paracypris***

Babinot *et al.*, 1983 - Provence

Curfsina Deroo, 1966,
Cytherella Jones, 1849,
Cytherelloidea Alexander, 1933,
Darwinula Brady & Robertson, 1885,
Dolocytheridea Triebel, 1938,
Dumontina Deroo, 1966,
Hazelina Moos, 1966,
Imhotepia Gründel, 1969,
Karsteneis Pokorny, 1963,
Limburgina Deroo, 1966,
Mauritsina Deroo, 1962,
Metacypris Brady & Robertson, 1870,
Neocyprideis Puri, 1952,
Oertliella Pokorny, 1964,
Paracandona Hartwig, 1899,
Paracyprideis Klie, 1929,
Parapokornyella Babinot, 1980,
Pterygocythere Hill, 1954,
Pterygocythereis Blake, 1933,
Risaltina Colin & Grekoff, 1973,
Trachyleberidea Bowen, 1953,
Valdionella Babinot, 1980,
Veeniaceratina Gründel & Kozur, 1972,
Xestoleberis Sars, 1866

Number of genera in this study = 24. Number of genera also seen in the present study = 10.

The present author created a stratigraphical range chart for the Coniacian to Lower Maastrichtian interval of Provence as listed by Babinot *et al.*, 1983 (fig. 1. 24). The fauna is markedly different from the Northern Realm of the Paris Basin and contains more genera which are not represented in the material of either the Trunch Borehole or the outcrop localities. In many cases, they also do not appear in any published British records. Of the 25 genera, fewer than half are seen in the material of the present study. Absent genera include *Dolocytheridea, Dordionella, Darwinula, Dumontina, Hazelina, Imhotepia, Karsteneis, Looneyellopsis, Metacypris, Neocyprideis, Paracandona, Paracyprideis, Parapokornyella, Risaltina, Valdoniella, Veeniaceratina* and others. As with Babinot 1980, the genera contain a certain freshwater element, with a transition from marine to freshwater observed in the Campanian. The assemblages of the present study are exclusively marine.

Fig. 1.24. Babinot et al., 1983 - Provence

CO	SA	CA	MA	genus
				Mauritsina
				Pterygocythere
				Cytherella
				Curfsina
				Trachyleberidea
				Parapokornyella
				Dumontina
				Dolocytheridea
				Limburgina
				Xestoleberis
				Oertliella
				Horrificiella
				Paracyprideis
				Pterygocythereis
				Veeniaceratina
				Dordionella
				Risaltina
				Hazelina
				Karsteneis
				Cytherelloidea
				Valdionella
				Metacypris
				Paracandona
				Ilyocypris
				Frambocythere

Babinot & Tronchetti - Provence:

The following genera are listed by the above authors:

Bairdia (=Bairdoppilata Coryell, Sample & Jennings, 1935),
Bythoceratina Hornibrook, 1952,
Chapmanicythereis Gründel, 1973 [= a junior synynym of *Platycythereis*],
Costaveenia Gründel, 1973,
Curfsina Deroo, 1966,
Cytherella Jones, 1849,
Cytherelloidea Alexander, 1929,
Dolocytheridea Triebel, 1938,
Dordoniella Apostolescu, 1955,
Hazelina Moos, 1966,
Horrificiella Liebau, 1975,
Kalyptovalva Howe & Laurencich, 1958,
Karsteneis Pokorny, 1963,
Limburgina Deroo, 1966,
Mauritsina Deroo, 1962,
Mosaeleberis Deroo, 1966,
Neocythere Mertens, 1956,
Occultocythereis Howe, 1951,
Oertliella, Pokorny, 1964,
Paracaudites Deroo, 1966
Paracyprideis Klie, 1929,
Parakrithe Van den Bold, 1958,
Parapokornyella Babinot, 1980,
Planileberis Deroo, 1966,
Pokornyella Oertli, 1964
Pterygocythere Hill, 1954
Pterygocythereis Blake,1933,
Risaltina Colin & Grekoff, 1973,
Schuleridea Swartz & Swain, 1946
Spinoleberis Deroo, 1966,
Uroleberis Triebel, 1958,
Veeniaceratina Gründel & Kozur, 1972,
Xestoleberis Sars, 1866

Number of genera = 33,
Number of genera also appearing in the present study = 16

The present author has not produced a range chart based on Babinot & Tronchetti's work on the Coniacian to Lower Maastrichtian ostracods of Provence. The fauna, when considered at generic level, conforms to previous studied of the region i. e. typically Tethyan Realm, with many Southern European genera and a freshwater component. It is unlike the Northern Realm faunas of the Paris Basin and , of the 33 genera, only 48% also occur in East Anglia.

Absent genera include *Costaveenia, Dolocytheridea, Dordionella, Hazelina, Hornificiella, Kalyptovalva, Karsteneis, Occultocythereis, Paracaudites, Paracyprideis, Pokornyella, Risaltina, Uroleberis, Veeniaceratina* and others.

Babinot *et al.*, 1983 - Aquitaine

Genera listed in the 1983 study are as follows:

Acuticytheretta Deroo, 1966,
Aequacythereidea (Mandelstam, 1947) [= a junior synonym of *Schuleridea* Swarrtz & Swain, 1946, according to the 1961 *Treatise*, Q284],
Annosacythere (Kuznetsova, 1957) =?[junior synonym of *Pleurocythere* Triebel, 1951],
Asciocythere Swain, 1952,
Bairdia (=Bairdoppilata Coryell, Sample & Jennings, 1935,
Brachycythere Alexander, 1933,
Curfsina Deroo, 1966,
Cythereis Jones, 1849,
Cytherelloidea Alexander, 1933,
Dolocythere Mertens, 1956,
Dumontina Deroo, 1966,
Echinocythereis Puri, 1954,
Eucytherura Müller, 1894,
Hemicytherura Elofson, 1941,
Hornificiella Liebau, 1975,
Imhotepia Gründel, 1969,
Kalyptovalva Howe & Laurencich, 1958,
Kikliocythere Howe & Laurencich, 1958,
Kingmaina Keij, 1957,
Krithe Brady, Crosskey & Robertson, 1874,
Limburgina Deroo, 1966,
Mauritsina Deroo, 1962,
Mosaeleberis Deroo, 1966,
Pseudobythocythere Mertens, 1956,
Spinoleberis Deroo, 1966,

Spongicythere Howe, 1951,
Trachyleberidea Bowen, 1953,
Uroleberis Triebel, 1958,
Veenia Butler & Jones, 1957

Number of genera present = 30
Number of genera also present in east Anglia = 13

The fauna of Aquitaine is even more typical of the Southern European Tethyan Realm and differs from those of Provence by the appearance of new genera.. Of the 30 species, most are rare or absent in published British records and only 43% are represented in the present study. Absent genera include *Accuticytheretta, Aequacytheridea [=Schuleridea], Annosacythere [=Pleurocythere], Dolocythere, Dumontina, Echinocythereis, Hemicytherura, Horrificiella, Imhotepia, Kalyptovallva, Kikliocythere, Kingmaina, Pseudobythocythere, Spongicythere, Uroleberis, Veenia* and others.

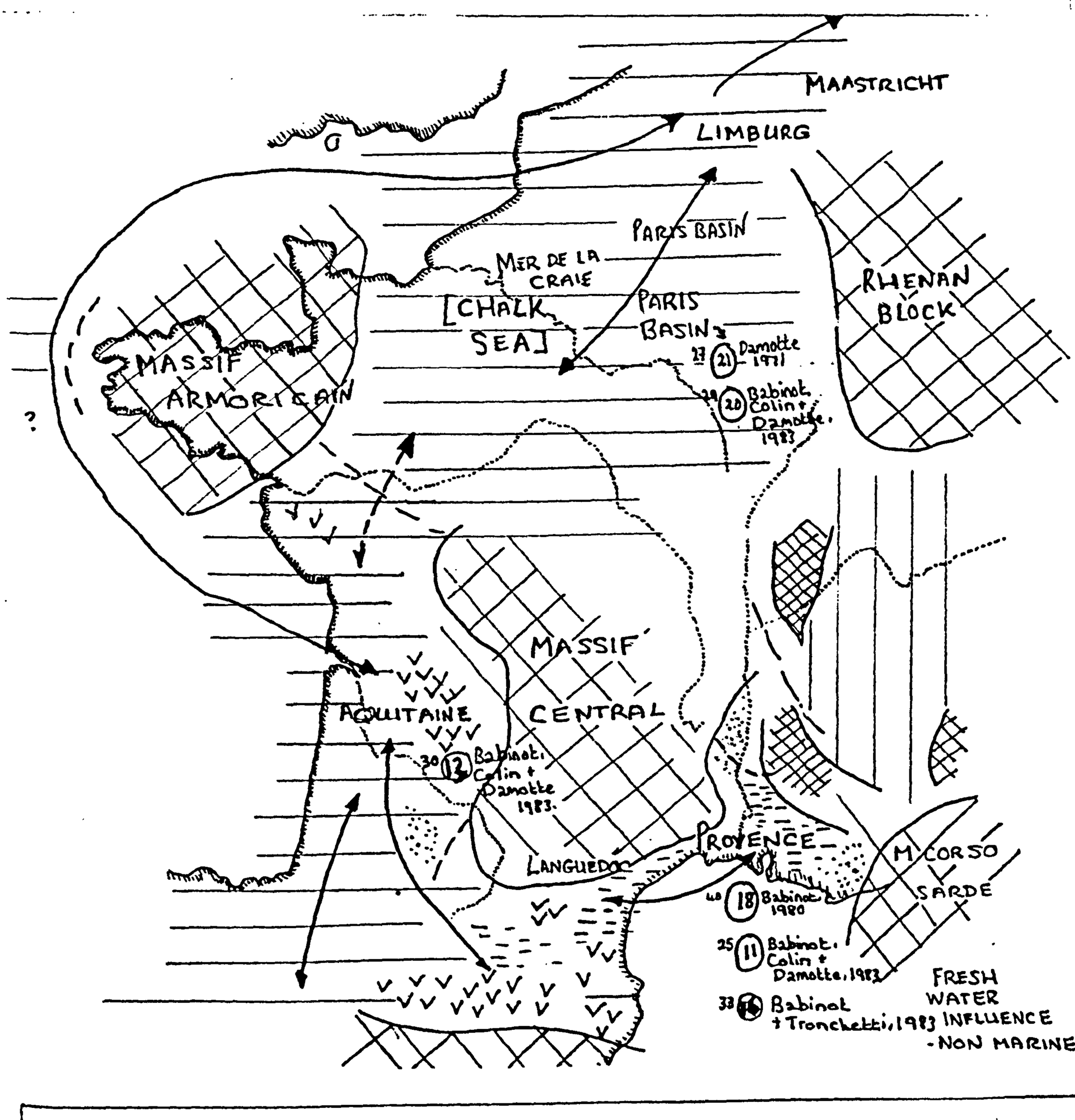
In Britain, the genus Veenia has been recorded up to the Cenomanian by Weaver, 1982, and other authors such as Kaye, 1964, and Neale, 1978. It does not appear in the Coniacian to Lower Maastrichtian in any British record or in the Paris Basin. This may represent a geographical shift to the warmer waters of the Tethyan Realm. *Veenia* (sensu lato) is only found in the Santonian and early Campanian of Aquitaine, wheras related genera or sub-genera such as *Veeniaceratina* have been recorded from similar intervals in Provence. This subject requires further investigation but was considered to be beyond the remit of this thesis. It will, therefore, not be discussed further and will be left for future research workers to resolve.

In summary, it has been proven that the Upper Cretaceous ostracod faunas of East Anglia are more comparable, at least on a generic basis. with those of the French Northen Realm (as characterised by the Paris Basin). They exhibit considerable differences, when contrasted with the Tethyan faunas of Southern France (as characterised by Provence and Aquitaine).

Figure 1. 25. is adapted from an earlier map published in Babinot *et al.*, 1985, which shows the palaeogeography of the French Upper Senonian. The present author has annotated this figure to show published studies in the Northern and Tethyan Realms.

Figure 1.25. . The palaeogeography of the French Upper Senonian, adapted from Babinot *et al.*, fig. 31, p. 217, to show previously published studies in the Northern Realm (Paris Basin) and the Tethyan Realm (Provence and Aquitaine).

The number enclosed within the circle is the number of genera that also appear in East Anglia, while the number outside the circle is the total number of genera listed in the study in question.



2) GERMANY

The Upper Cretaceous Ostracoda of Germany have been studied by such authors as Gründel, 1968a, 1968b. 1969, 1970; Ohmert, 1973 and Clarke, 1983. The last mentioned of these authors, however, studied only the Cytheracea from the Coniacian to Maastrichtian of Northern Germany. In general, German faunas are closer to the French Northern Realm (Paris Basin) than the Tethyan Realm (as represented by Provence and Aquitaine), but contain fewer "warm water" genera and fewer genera as a whole. Some genera not recorded in the French studies (e.g. *Schizocythere, Paijenborchella, Hemicytherura, Idiocythere, Eucythere, Argilloecia* and *Saida*) appear in German Chalks of a similar age. Of these genera, only *Hemicytherura, Paijenborchella, Isocythereis* and *Idiocythere* were not represented in East Anglia. The German material, especially that studied by Herrig, 1967, is very similar in its generic composition to the faunas seen in East Anglia.

I) Northeastern Germany - Herrig, 1967, Coniacian to Lower Maastrichtian.

Herrig records the following genera:

Amphicytherura Butler & Jones, 1957,
Argilloecia Sars, 1866,
Bairdia = *Bairdoppilata* Crosskey, Sample & Jennings, 1935,
Bythoceratina Hornibrook, 1952,
Cytherelloidea Alexander, 1929,
Cytherella Jones, 1849,
Cythereis Jones, 1849 - Herrig includes several forms which should be reassigned to *Curfsina, Limburgina, Planileberis, Rehacythereis.*
Eucytherura Müller, 1894,
Hemicytherura Elofson, 1941,
Idiocythere
Isocythereis Triebel, 1940,
Krithe Brady, Crosskey & Robertson, 1847,
Neocythere Mertens, 1956,
Paijenborchella Triebel,
Phacorhabdotus Howe & Laurencich, 1958,
Saida Hornibrook, 1952,
Schizocythere Triebel, 1940.

17 genera are recorded, of which 13 also appear in the material of the present study. Herrig, however, does not distinguish between forms previously assigned to Cythereis which are now reassigned to various different genera. If these genera are divided, Herrig actually records 21 genera, of which 17 are present in the Upper Chalk of East Anglia.

ii) Ohmert 1973 - Santonian.

Ohmert, 1973, working with Santonian samples from the Gehrdener Berg, near Hannover, notes that the faunas are "only comparable with the faunas of the Maastrichtian of Limburg as to the composition an drichness of species." He discusses the ecological shifting of the faunal distribution in a series ranging from transgressive facies to sublittoral environments. The assemblages were "rich in species but poor in specimens." In the present study, especially in the outcrop localities, both specific diversity and number of individuals present in each assemblage are low, attributed to low oxygen levels. Ohmert's assemblages show no evidence of intervals of lowered oxygen. 57 species belonging to 35 genera were reported, but the full generic list will not be given here.

3) Demnark, Belgium and South Limburg, Netherlands.

The Ostracod faunas in previous studies (Van Veen, 1928, 1932, 1936; Bless, 1988a, 1988b; Bless & Robaszynski, 1988; Jørgensen, 1978, 1983; Robaszynski et al., 1985, and others) are quite similar to those of East Anglia in their generic composition. There has, however, been relatively little work on continuous sections of Coniacian to Lower Maastrichtian; the majority of studies have concentrated on one particular interval. Van Veen produced a series of papers on the "Maastrichter Tuffkreide" of Southern Limburg (1932, 1934, 1935, 1936a, 1936b, 1938) but these are largely taxonomic in nature with each paper detailing a specific family or taxonomic group.

Jørgensen (1983) writes that the "ostracodes recorded from the Maastrichtian White Chalk in the Danish sub-basin constitute a rich and highly diverse fauna of 95 species, representing 34 genera." The fauna is dominated by mid-outer shelf genera (*Bairdia, Cytherella, Cytherelloidea)* although deeper water taxa (e.g. *Krithe, Argilloecia, Bythoceratina*) are relatively abundant. The full generic list is given in an earlier paper (1978) and also in a 1970 unpublished thesis, unavailable o the present author, which dealt with the Ostracoda of the Danish "Skrivekridt", an interval assumed to correlate with the Maastrichtian Schreibkreide and the White Chalk of Limburg.

HINGEMENT IN THE OSTRACODA

A detailed discussion of each hinge type is given by such authors as Sylvester Bradley, 1956; Howe & Laurencich, 1958; Van Morkhoven, 1962, p. 72-82; *Treatise on Invertebrate Paleontology,* Part Q, Ostracoda, 1961, and many other more recent authors. The exact definitions that compromise each hinge type will not be presented here, to avoid unnecessary repetition.

The taxonomic importance of the ostracod hinge:

Many authors have stressed the importance of the hinge structure in ostracod classification. It is of great taxonomic value on a generic and familial level, and is also of use in studies of comparative morphology. Van Morkhoven (1962, p. 79) makes the valid point that "apart from the hinge, many other

structural elements of the valves will have to be taken into account when trying to classify ostracods into true phylogenetic - monophyletic taxa." Although the "same hinge=same genus" generalisation of certain authors (e. g. Mandelstam) must logically be incorrect, it is more feasible that the idea of same genus = same hinge may be accepted when "hinge" is taken to mean hinge type. This, however, only applies to adult specimens. Juveniles have an entirely different and much simpler hinge, only developing the true adult hingement in the pre-maturation moult. In the Cythereideinae, for example, most genera share a common antimerodont larval hinge (see Sandberg, 1964, p. 358 and this thesis, fig. 1.26). In genera where the adult hinge is also antimerodont, as in the genus *Clithrocytheridea,* there is no change during the final moult maturation, as in the genus *Haplocytheridea,* the antimerodont juvenile hinge undergoes a reversal of the median element. In the amphidont hinge type group, the degree of development of the structural element is of prime importance in the identification of juvenile and adult specimens.

Van Morkhoven (1962, p. 89-90) considers the amphidont hinge to be an exclusively adult development. A clear subdivision of the median hinge elements does not take place in any of the juvenile stages. The hinges in such forms, in the later ontogenetic stages, remain clearly merodont while, in the younger instars, the hinge is either adont or weakly merodont. The assumption that specimens with an amphidont hingement are exlusively adult should only be applied to genera where the hinge is amphidont. Those valves with a merodont hinge may be juveniles of a typically amphidont species (and identifiable as such by observations of size, shape, ornament and internal structure such as the width of the inner lamella) or adults of a non-amphidont species.

Minor differences that do not affect the designation of hinge type include stronger or weaker development of the hinge element, the presence or absence of crenulation or lobation of one or more elements. Such characteristics may be highly variable in the different species of any one genus. Van Morkhoven (1962, p. 80) considers that the presence or absence of an accommodation groove is "the inevitable consequence of any considerable difference in size between the two valves." Since this feature may vary within a genus, the presence of an accommodation groove is not always a criterion to be used in separating genera.

In the distinction of "suprageneric systematic categories", hingement is of relatively minor importance, especially in the case of certain subfamilies of the Cytheridae. Van Morkhoven writes that the "numerous variations of the amphidont hinge type occur exclusively in this family, and any genus possessing an amphidont hinge type may safely be assigned to it." the same author also makes the point, however, that the family also comprises a number of genera with a merodont hinge. No hinge type should be restricted, therefore, solely to one subfamily. Since merodont hinges also occur in the Cyprididae, together with the more common adont morphology and, as a general rule, these hinge types do not exhibit as much variety as the amphidont type, they are "similarly of little value" as a criteria for distinguishing subfamilies.

The relationship between hinge morphology and "mode of life".

There is a clear relation between hinge morphology and the degree of development of the hinge and the mode of life. Groups that adopt a swimming habit can be identified by th adaptation of certain soft part, for example the long natatory setae present on the first and second antennane in the Halocypridae and most Cyprididae, which are not seen in the non-swimming forms such as the Cytheridae. Such structures are not preserved in the fossil record, the calcareous valves being the only parts available for study. Swimmers can easily be distinguished from those forms which burrowed or walked, with reference to the structure of the hinge. Extant forms of any particular genus known for its swimming habit can be assumed to have had a similar mode of life in the past. Swimming forms usually show a weak to very weak hinge which is frequently short and adont. The marine Bairdiidae show a weak lophodont hinge. Stronger hingement, which comprises the majority of hinge types seen in the present study, with long hinge lines and strong crenulate hinge elements are found only in the marine Cytheridae, especially in the Trachyleberinae which are typically bottom dwelling, crawling forms. A stronger valve connection is needed due to the increased pressures of this lifestyle. The bottom dwelling Platycopa, with the exeption of the adont genera *Cytherella* and *Cytherelloidea,* all possess a more or less well-developed hinge.

Morphological and morphogenetic trends in ostracod hingement:

Well-differentiated hinge structures are especially characteristic of the Cytheridae, which in Post-Palaeozoic times provided a far greater number of representatives than all the other groups combined. Van Morkhoven (1962, p. 161) states that all types of hinge may be encountered among the recent representatives of the family but that the hinge was, in general, of a much simpler configuration at the beginning of the Mesozoic. Present day structural variation was acquired gradually throughout the post-Palaeozoic. By the Upper Cretaceous, the development of the hinge was quite well advanced. Merodont species of *Protocythere* are replaced by *Protocythere*-like amphidont species and *Veenia*. Genera such as Amphicytherura and Pterygocythereis appear gradually and, in the Senonian, amphidont genera such as *Brachycythere, Haplocytheridea, Phacorhabdotus* appear, together with the last paramphidont hinged species of true *Cythereis*; a genus restricted by Sylvester-Bradley, 1948, to the Cretaceous.The first Cytherettinae appear (e.g. *Paracytheretta* and *Buntonia*) as well as schizodont genera such as *Paijenborchella* and *Schizocythere*. The most primitive of Palaeozoic ancestral hinges was adont but, before the start of the Mesozoic, both smooth and crenulate merodont hinges had developed. Among early Mesozoic Cytherids the merodont / entomodont hinge type predominates. During the Middle Jurassic, many different groups of Cytheridae began to exhibit a sub-division of the median hinge element and eventually developed a well developed "archidont hinge". This is a term proposed by Van Morkhoven (1962, p. 76, 162) to mean a hinge "transitional between the merodont and true amphidont types." This type of hinge, in Sylvester-Bradley's terminology is referred to as entomodont. In the archidont / entomodont case subdivision of the median element is not pronounced.

The anteromedian hinge element is never developed into a tooth, differing from the postero-median one only in being more coarsely crenulate. The anterior element is always notched; the

posterior element is usually the same, but may be smooth. Examples of "archidont" hingements include *Progonocythere* (but see Whatley & Ballent's 1996 revision of the Progonocythereidae) and *Oligocythereis*. Hence, Late Middle Jurassic assemblages may be recognised by the predominance of such hinges and the absence of true amphidont types. The first amphidont / heterodont hinge developed in the Upper Jurassic with a few genera such as *Amphicythere*, but it is not common before the Cretacous, where it is found in many different genera (e.g. *Cythereis, Platycythereis* and *Isocythereis*). In the Cretaceous, the archidont hinge is less common, although Van Morkhoven and other authors note that "a parallel evolution of a heterodont / entomodont hinge via an archidont stage into a clearly amphidont hinge takes placein certain groups", e.g. the *Pleurocythere - Protocythere - Veenia* phylogenetic lineage.

The schizodont hinge developed during the Late Cretaceous (e.g. some species of *Amphicytherura , Paijenborchella and Schizocythere*. In the present study, this type of hinge is outnumbered by genera with a merodont or amphidont hingement, but the schizodont hinge is extremely well developed in the material from Coniacian to Lower Maastrichtian of East Anglia, suggesting that the hinge evolved rapidly into an advanced state of development. A new species described in this present work, restricted to the Lower Maastrichtian outcrop samples of Trimingham, Norfolk, shows a typical schizodont hinge; *Schizocythere biponticulata* (sp. nov.) has, in the right valve, a stepped anterior tooth increasing in height proximally anteriorly, with a strongly bilobate posterior tooth. the median element is very strongly locellate postero-medianly with a strongly bi-locullate socket. Complementary structures in the left valve occur; above the median element is a long, gutter-like accomodation groove.

Gongylodont hinge structures, such as are shown by such genera as *Loxoconcha* are not seen in the present study, although Weaver, 1982, and Wilkinson, 1988, report species of this genus as present in the plenus marls and Cenomanian and Upper Jurassic, Lower Cretaceous respectively. In the material of the present study, one species was seen which closely resembled published species of *Loxoconcha*; such forms, however, showed clear gongylodont hingement and the species seen in this study appeared to have a simple, lophodont hinge. It appears in the systematic taxonomy as a new species of the genus *Sagmatocythere*.

If the hingement of the material studied by the present author is categorized, it becomes clear that the most common hinge types are merodont (at least 11 genera) and amphidont (at least 8 genera). A further 8 genera show simple or adont hinges, at least two show lophodont dentition and two exhibit schizodont hinges. This is to be expected in the Late Cretaceous when hinge development was quite advanced.

Damotte (1971a, pp 46-47) discusses in detail the genus *Protocythere* and the relationships with *Mandocythere* and *Costacythere*, with reference to hinge structure. *Mandocythere* (Grundel, 1964) differs essentially from the first genus by its paramphidont hinge; *Protocythere* and *Costacythere* both show antimerodont hinges. The former author also presents a table (tb. 9, p. 47) contrasting and comparing the principle characteristics of the three genera. Evolutionary lineages are also drawn, tracing the development from an ancestral *Protocythere* in theUpper Jurassic. The genus *Protocythere* appears to range from the Kimmeridgian up into the Cenomanian (Van Morkhoven, 1962, p. 222); hinge structure is merodont/ entomodont according to Van Morkhoven and antimerodont in Damotte's analysis. In the right valve, the

toothlets of the anterior and posterior teeth often show a secondary crenulation, as in the genus *Pleurocythere* Triebel, 1951; a possible ancestor. *Protocythere* differs in the ornament and in the hinge (all elements are crenulate and grade smoothly into each other). The Upper Cretaceous Veenia differs in its amphidont hingement. Van Morkhoven, having discussed the *Protocythere* - *Veenia* lineage as a given fact only a few pages earlier (p. 223), also states that the latter is "probably an Upper Cretaceous offspring of some Lower Cretaceous *Cythereis*, rather than a descendant of *Protocythere*" 1962, p. 229) It is not clear which the author intends to be accepted - both scenarios are presented equally. However, many other authors have documented phylogenetic links between the Jurassic *Protocythere* and the Late Cretaceous *Veenia*.

Wilkinson (p. 337, MS), writing in 1988, discusses the Protocytheridae as a family which has had a confused taxonomy in the past, especially at generic level. This appears largely due to Grundel (1964, 1966, 1974). The latter author erected several genera and sub-genera based principally on relatively minor differences in ornament. Wilkinson includes such genera as within the Protocytheridae, and recognises four subfamilies based on ornament and the structure of the hinge: the Protocytherinae to include those genera with a antimerodont hinge (see Wilkinson, 1988, p. 339, for details of ornament) e.g. *Protocythere, Costacythere* ; the Mandocytherinae to include those genera which differ only from the previous sub-family in their amphidont hingement - e.g. *Mandocythere*. The Pseudoprotocytherinae also have amphidont hinges but differ markedly in their ornament; lastly the subfamily Pleurocytherinae accomodates genera with a "strikingly multicostate ornament and an antimerodont to hemimerodont hingement. Wilkinson agrees with Van Morkhoven, 1962, in that the "origins of the latest Jurassic and Cretaceous Protocytheridae lie within the Pleurocytherinae."

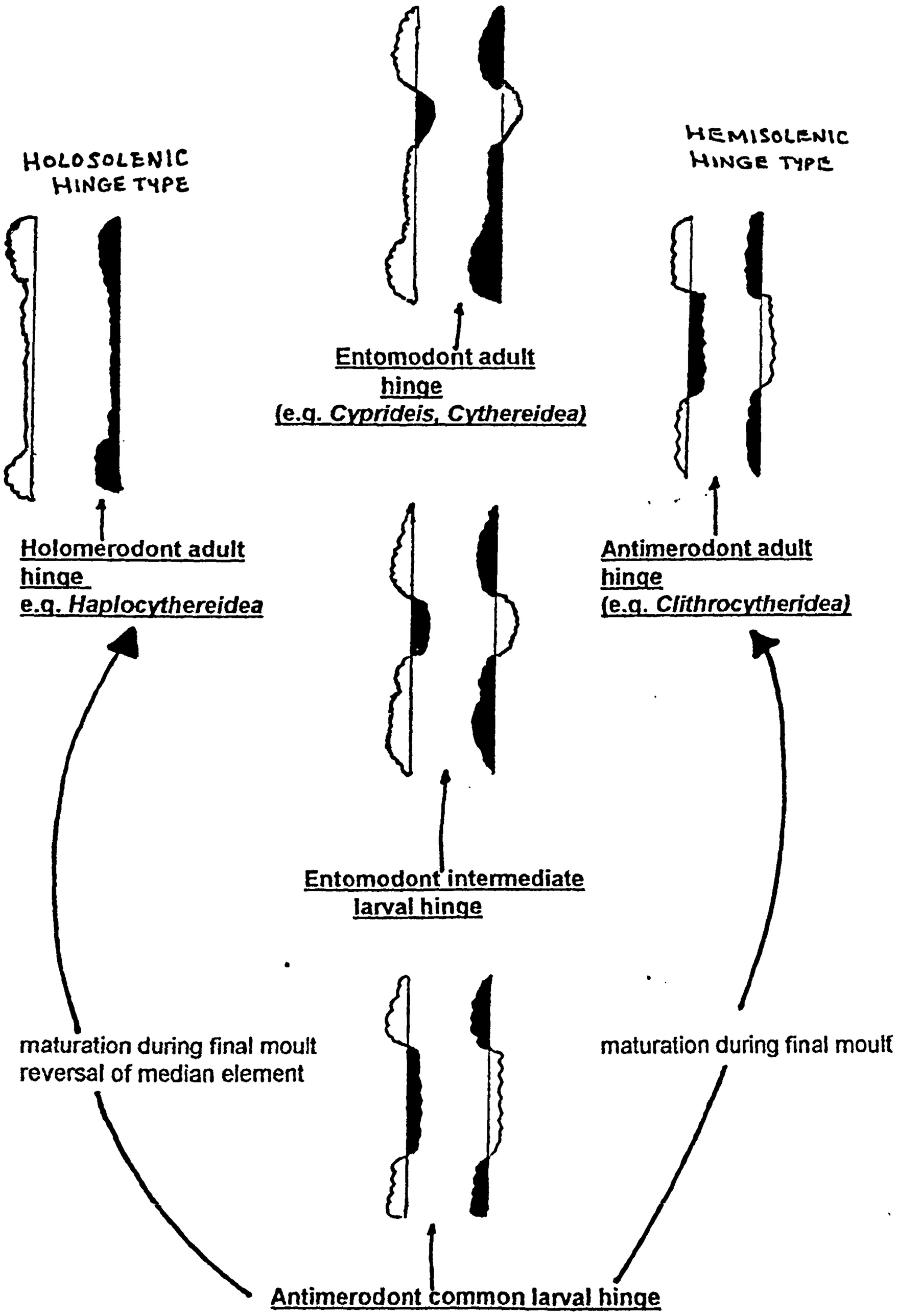
The Protocytheridae are generally considered to have become extinct before the end of the late Cretaceous; certainly no representatives are seen in the Coniacian to Maastrichtian of the present study. It is doubtful that the family survived beyond the Cenomanian - Turonian Boundary. A major event in Protocytherid development appears to have occurred at the end of the Barremian or early Aptian, when amphidont genera of the Mandocytherinae first appeared. The earliest of these is the genus *Mandocythere* itself which is a "heavily calcified, subrectangular form with sub-parallel dorsal and ventral margins, three thick, straight longitudinal ribs and a modified paramphidont hinge. Since the genus *Protocythere* and related forms do not appear in the material of the present study, there is no need to discuss it further; it was included in this thesis merely to emphasise the usefulness of the hinge in distinguishing between several very similar genera within a phylogenetic lineage. A single specimen was tentatively assigned to *?Protocythere* sp.

The evolution of the Cytheracean hinge passes through three distinct stages, begining with the acquisition, from a primitive smooth hinge, of crenulations in the anterior and posterior terminal elements. Such crenulations "increase in strength in early evolutionary series to form separate toothlets and coalescing in later stages until they revert to a smooth phase" (Sylvester-Bradley, 1948, pp. 796-797). The other two trends are as follows:

1) The subdivision of the median element

2) The development of secondary crenulations on the median bar.

Fig.1-26 : Hinge ontogeny in the Cythereideinae (adapted from Sandberg, 1964, p. 358, fig. 1)



Hinge morphology and ontogeny in the Cytherideinae

Sandberg, 1964, in examining larval - adult relationships in some species of the genus *Haplocytheridea*, writes in the opening paragraph " the antimerodont hinge seems to be the common larval hinge of the Cytherideinae, regardless of the adult hinge type. This suggests that the primitive hinge of the Cytheracea is the hemisolenic type (e.g. antimerodont) rather than the holosolenic type (e.g. holomerodont) proposed by Pokorny (1957). The occurrences of holosolenic hinges in advanced groups with hemisolenic hinges, such as the Cytherideinae, is considered to be an innovation rather than a retention of ancestral characters" (Sandberg, 1964, p. 357). The same author also examined larval and adult hinges of numerous species in 5 other genera, including *Clithrocytheridea.* In all of these genera, the juvenile hinge is antimerodont; the adult hinge in *Clithrocytheridea* is also antimerodont, in *Haplocytheridea*, *Cyamocytheridea* and *Eucytheridea*, the antimerodont hinge is transformed during the last moult stage by a reversal of the median element. Sandberg discusses Pokorny's earlier work on the phylomorphology of the podocopid hinge. In a holosolenic hinge type, all positive elements are in one valve and all negative elements in the opposite valve. The hinge is an elaboration of an unbroken contact rim in one valve and an unbroken contact groove in the other. In a hemisolenic hinge, the contact groove is "interrupted by the fusing of its delimiting structure or by the formation of a ridge - or bar-like protuberance in the middle hinge (Sandberg, 1964, p. 358, quoting from Pokorny, 1957, p. 5).

Pokorny concluded that podocopid ostracods arose from a "holosolenic platycopa ancestor" and that, in many podocopids, "a modified holosolenic contact margin has been retained even in the morphologically advanced Cytherideidae, where it coexists with the hemisolenic type in some sub-families (the Cytherideinae). According to the 1964 paper, it is not the holo- but rather the hemisolenic (antimerodont) hinge that is the primitive or original type occurring as the larval hinge of the Cytherideinae and carrying through into the adult form of more than half the genera of that subfamily (e.g. *Clithrocytheridea* and others). Sandberg (p. 359) states that the "primitive hinge type, which has carried through the phylogenetic development of the Cytheracea, is the hemisolenic (antimerodont) type.....Hemisolenic hinges characterize the moults of many genera which have amphidont adult hinge structures. Hemisolenic hinges are virtually universal in some of the earlier Cytheracea, particularly the Progonocytherinae: believed to be the ancestral group for many of the post-Mesozoic Cytheracean Ostracoda."

The family Cytherideidae: an evaluation of the taxonomical position of the forms in the present study:

Kaye (1963c), in a re-evaluation of the Mesozoic genera of the Cytherideidae, identifies the valid genera within the disordered nomenclature and uncertain generic recognition with the aim of "interpreting their inter-relationships and to correct higher taxonomical assignments" (p. 23).

Some difficulty has been encountered in interpretation. The genera within the Cytherideinae are separated on the basis of minor details in shape and hinge structure. In the material of the present study, the species could be assigned to one of several genera; the details of the hinge not always being clear.

To confirm the identity of these species, it is necessary to take each genus in turn and work through them systematically using generic descriptions and comparisons with type and/or representative species.

Sub-family CYTHERIDEINAE Sars, 1925 , range = Lower Cretaceous - Recent.

Stephenson (1936), in an important paper on the shell structure of the genus *Cytheridea,* shows that "many forms then referred to *Cytheridea* on the basis of shape, differed significantly in their hinge structure from the genotype". The two sub-genera *Haplocytheridea* and *Clithrocytheridea* were erected to accommodate them (see also Kaye, 1963c, p. 25). The former author raised both sub-genera to full generic status in a later publication (1946). Other related genera have been found in the Tertiary, but the only Mesozoic species referred to the group belong to either *Haplocytheridea* or *Clithrocytheridea.* The latter genus is very common in British and European records (e. g. Kaye, 1963c, 1964b; Kaye & Barker, 1965, 1966; Gründel, 1966, Damotte, 1971a ; Weaver, 1982; Wilkinson, 1988; Witte *et al.,* and others) from the Albian to the Lower Maastrichtian.

Genus CLITHROCYTHERIDEA Stephenson, 1936

Kaye (1963c, p. 26): "the hinge in the left valve consists of two elongated divided sockets, separated by a finely denticulate bar. An accomodation groove is either present or absent. The hinge is anti-merodont." The shape is generally sub-quadrate and the surface can be smooth or pitted. In the type species (*Cytheridea? garreti* Howe & Chambers) and other Tertiary forms, the pore canals are straight and numerous. Lower Cretaceous members, although of typical shape and hingement, have fewer radial pore canals. The characteristics of this genus, especially hinge type, would place at least two of the species in the present study firmly within *Clithrocytheridea,* but certain other morphological features preclude this diagnosis. All Cretaceous representatives of the genus seen in published records have an elongate shape; the present material shows an arched dorsal margin and tumid carapace.

Sub-family SCHULERIDEINAE Kollman, 1960.

The genera in this sub-family have a similar shape and hingement to members of the Cytherideinae but differ in the nature of their pore canals. They also usually have a well-developed eye tubercle with a shallow sulcus posterior to it and strong accommodation grooves in the left valve (Kaye, 1963c, p. 26). Although the original interpretation of the hinge within this subfamily restricts it to forms with all positive elements in the right valve and the median element undivided, some Cretaceous species of *Schuleridea* do have divided median elements. To base the sub-family on minor details of hinge morphology would exclude many otherwise similar genera. In a revision of Mesozoic Cytherideidae, Kaye prefers not to restrict the Schulerideinae to forms with a "rigidly specified hinge structure" but includes other forms with a hingement similar in basic pattern but differing in certain minor details. The characteristic genus is *Schuleridea.* Genera such as *Asciocythere* Swain and *Apatocythere* (Triebel) also belong in this subfamily.

Genus SCHULERIDEA Swartz & Swain, 1946.

Kaye (1963c, pp 26-27) notes that "the poor preservation of the American Upper Jurassic species of this genus (type species = *Schuleridea acuminata*) made the detail of the hinge and marginal areas uncertain. Originally, it was thought that the median hinge element in the left valve was a smooth bar but the better preservation of European species allowed a good description to be made of the hinge in these forms but the exact nature in the type species is still uncertain." The European representatives of the genus have, in the left valve, two terminal elongated crenulate sockets joined by a narrow, smooth or finely locellate groove. Above the median element is a high, smooth bar followed by a broad accommodation groove. From an examination of the published Cretaceous species, it becomes clear that one of the most important diagnostic features is the presence of an eye tubercle. The species that occur in the present study, although strongly resembling *Schuleridea* in size, shape and the smooth or pitted ornament, show no evidence of either external ocular tubercles or internal ocular sinuses. They cannot, therefore, be assigned to this genus.

Genus APATOCYTHERE (Triebel)

The members of this genus are almost identical to *Schuleridea* in shape and external appearance, marginal features and muscle scars, but differ markedly in hinge structure. In the right valve, the hinge consists of a high, smooth anterior tooth and a smooth, triangular posterior tooth joined by a narrow smooth bar (Kaye, 1963c, p. 28). The left valve is complementary to the right valve, with a broad accommodation groove.

Initially, the material of the present study was mostly assigned to this genus, some of the species appearing almost identical to *Apatocythere simulans* of Triebel (Kaye, 1963c, pl. 1, figs 17-19; pl. 3, figs 1-7) and several other Cretaceous species. Under further examination, however, it became clear that such forms could not belong to this genus, since both the median and terminal elements of the hinge are crenulate.

Genus ASCIOCYTHERE Swain, 1952.

The hinge of this genus consists of, in the left valve, two terminal crenulate sockets separated by a smooth bar. Above the median bar is a broad accommodation groove. The genus is generally less elongate and sub-quadrate than *Clithrocytheridea*. The species of the present study were assigned to this genus on the basis of their shape and hinge structure. The hinge is more similar to Clithrocytheridea than in the type species.

Figures 1. 27 illustrates the hinge type and certain other diagnostic characteristics of *Asciocythere* (A), *Schuleridea* (B), *Apatocythere* (C) and *Clithrocytheridea* (D)

Fig. 1.27.

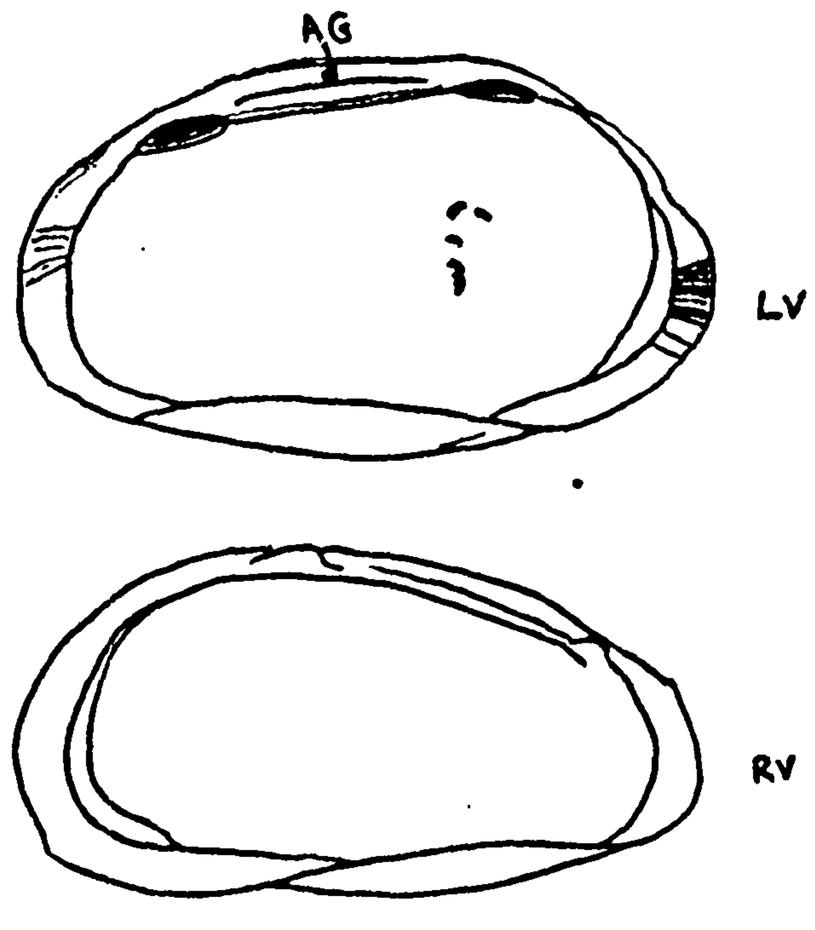
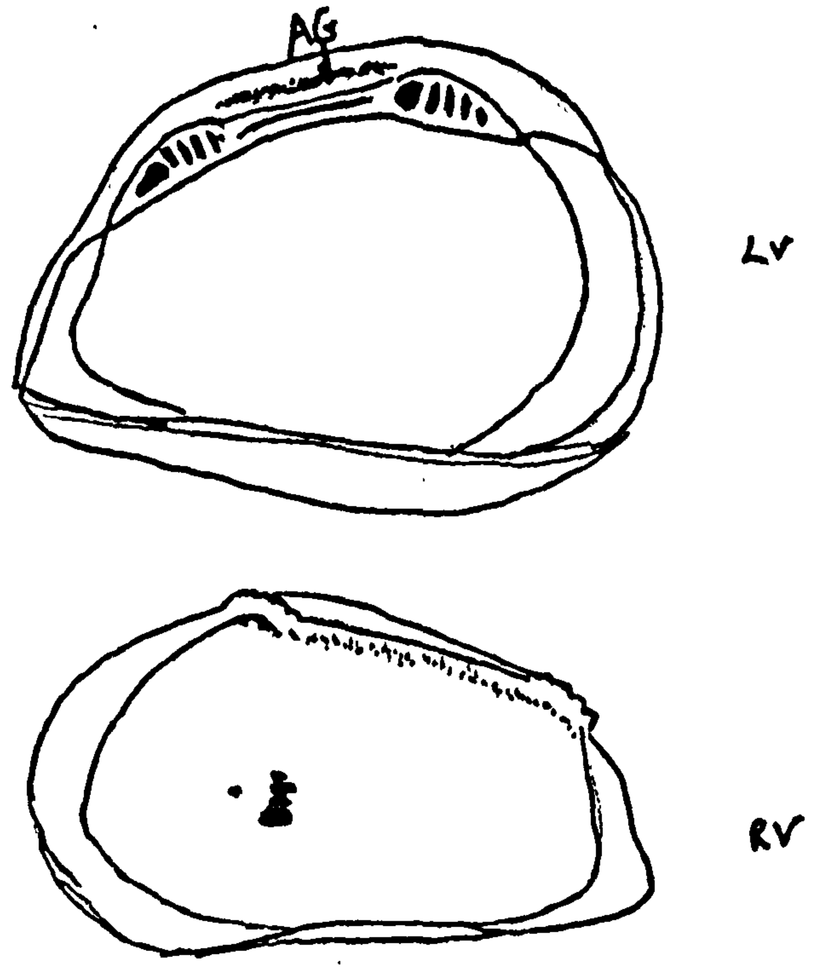
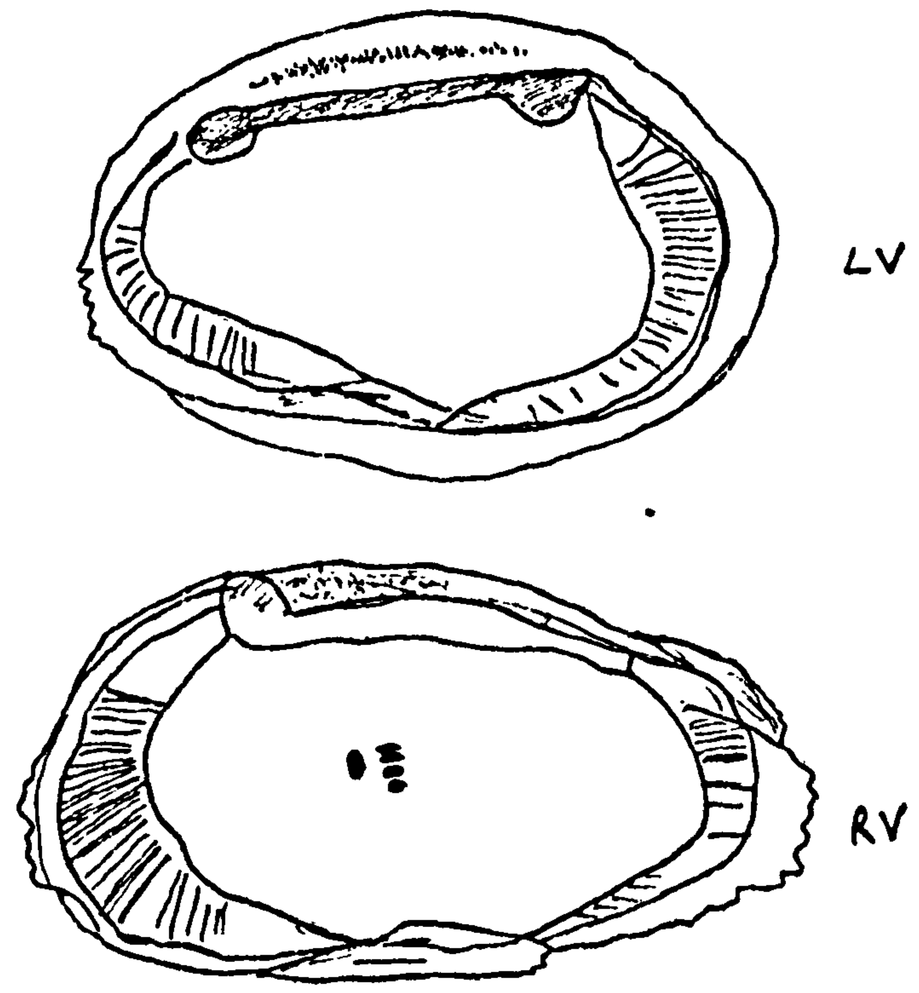
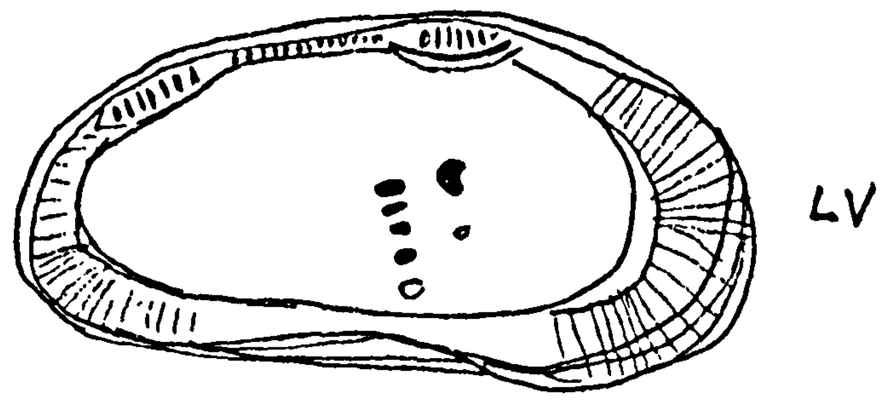
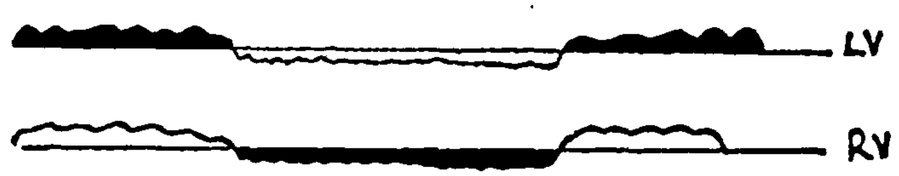
A) Genus **ASCIOCYTHERE** Swain, 1952	B) Genus **SCHULERIDEA** Swartz & Swain, 1946
	
Asciocythere polita Damotte, internal view x 85 Damotte, 1971a, text fig. 20, p. 107 - Turonian, Paris Basin	*Schuleridea bernouilensis* Grosdidier, internal view x 60, Damotte, 1971a, text fig. 22, p. 111
Treatise reference: Q273, description of genus: "LV with crenulate terminal sockets separated by a smooth median bar, above which is a well-defined accommodation groove. Marginal areas narrow with numerous radial pore canals"	Treatise reference: Q284, description of genus: "LV hinge originally described with crenulate terminal sockets and an unknown median element but (as figured by another Triebel species) shows a straight, smooth median furrow, above which is an accommodation groove (AG); muscle scars in a row of 4 with one in front of middle."

Fig. 1.27 (continued):

C) Genus <u>APATOCYTHERE</u> Triebel, 1940	D) Genus <u>CLITHROCYTHERIDEA</u> Stephenson, 1936
	
type species: *Apatocythere simulans* Triebel, internal view (slighly enlarged from Van Morkhoven, 1963 text figs 491, 492, p. 311 - Barremian of Germany	type species: *Clithrocytheridea lerichei* Keij, internal view (from Van Morkhoven, text fig. 441, p. 283 - Eocene of France
	
Treatise reference: Q262, description of genus: "Hinge amphidont (except that anterior socket of RV and tooth of LV are lacking); marginal areas broad with numerous radial canals on the anterior part that curves above middle, muscle scars in a vertical row of 4, with a single scar in front."	Treatise reference: Q276, description of genus: "Hinge antimerodont, LV with terminal crenulate sockets separated by raised crenulate bar; marginal area fairly broad, with numerous radial canals; muscle scars in a vertical row of 4 with 'V' shaped antennal scar in front and two oblique mandibular scars below."

CHAPTER 2. SYSTEMATIC TAXONOMY.

GENERIC TYPE SPECIES.

The Rules of Zoological Nomenclature (discussed extensively in the Editorial Preface (Moore & Pitrat, 1961) , of the *Treatise of Invertebrate Palaeontology*, Part Q- Ostracoda) provide that the type species of a genus or sub-genus may be recognised as an **original designation** if only a single species was assigned to the genus at the time of first publication (**monotypy**). If the original author explicitly indicated the species chosen as the type, or if some other stipulations were met. According to conventions adopted in the *Treatise*, " the absence of any indications as to the manner of fixing the type species is to be understood as signifying that it is established by original designation, the particular mode of original designation not being specified. Genera with type species by original designation include *Aversovalva*, *Cytherelloidea*, *Macrocypris*, *Paracypris*, *Pontocyprella*, *Bythoceratina*, *Pterygocythereis*, *Curfsina*, *Cytheropteron* and others. Genera in which the type was established by monotypy include *Monoceratina*, *Neocythere*, *Matronella*, *Oertliella* and others. The type species of many genera are not determinable from the publication in which the generic name was first introduced and, therefore, such genera can acquire a type species only by some manner of **subsequent designation** (e.g. *Xestoleberis*, *Cytherella*, *Cythereis*, *Eucytherura* and others). Most commonly, this is established by publishing a statement naming as the type species one of the species originally included in the genus. Some genera, as first described and named, include no mentioned species and these necessarily lack a type species until a date subsequent to that of the original publication - when one or more species are assigned to such a genus. If only a single species is assigned, it automatically becomes the type species and definition of the type species is by **subsequent monotypy.**

A checklist of type species for some of the genera seen in the present study:

(*C indicates that the type is a Cretaceous species)

a) By Monotypy:

Aversovalva Hornibrook, 1952 = *Cytheropteron (Aversovalva) aureum* Hornibrook, 1952, p. 57, from the Tertiary of New Zealand.

Neocythere Mertens, 1956 *C = *Neocythere vanveeni* Mertens, 1956, p. 205, pl. 12, figs. 72-78; pl. 14, fig. 100-102, from the Upper Albian of Lingen, West Germany (see Kaye, 1963).

Matronella Damotte, 1974 *C = *Cythereis matronae* Damotte & Grosdidier, 1963, p. 57, pl. 3, fig. 7a-f, from the Upper Albian of Haute-Marne, France.

Monoceratina Roth, 1928 = *Monoceratina ventrale* Roth, 1928, Carboniferous, Oklahoma, USA.

Oertliella Pokorny, 1964a *C = *Cythere reticulata* Kafka, 1886, from the Upper Turonian of Bohemia, Pokorny, 1964a, p. 283 (see also Benson, 1972).

Schizocythere Triebel, 1950 = *Schizocythere hollandica* Triebel, 1950, p. 322, pl. 2, fig. 17; pl. 3, fig. 18-19, from the Upper Miocene of the Netherlands.

b) **By original designation:**

Amphicytherura *C Butler & Jones, 1957 = *Cytherura ? dubia* Israelsky, 1929, p. 6, pl. 4a, fig. 6, Upper Cretaceous of Arkansas, USA.

Argilloecia Sars, 1866 = *Argilloecia cylindrica* Sars, 1866, recent, Norway.

Bairdoppilata Coryell, Sample & Jennings, 1935, = *Bairdoppilata martyni*, Miocene of Mississippi, USA.

Bythoceratina Hornibrook, 1952 = *Bythoceratina mestayerae*, recent, New Zealand.

Brachycythere *C Alexander, 1933 = *Cythere sphenoides* Reuss, 1854 from the Senonian of Austria.

Cuneoceratina *C Gründel & Kozur, 1971 =*Cythere ? pedata* Marsson, 1880, Upper Chalk, Germany.

Curfsina *C Deroo, 1966 = *Curfsina major* Van Veen, 1936, Deroo, pl. 6, figs 33-38, Maastrichtian, Holland.

Cytherelloidea *C Alexander, 1929 = *Cythere (Cytherella) williamsoniana* Jones, 1849, p. 31, pl. 7, fig. 26a-h, British Cretaceous.

Cytheropteron Sars, 1866 = *Cythere latissima* Norman, 1865, recent, North Atlantic (= *Cytheropteron convexum* Sars, 1866).

Hemiparacytheridea *C Herrig,1963 =*Paracytheridea (Hemiparacytheridea) occulta* Herrig, 1963, p. 299, pl. 3, fig. 5-9, text fig. 15, 16, from the Lower Maastrichtian of Rugen, Germany.

Macrocypris Brady, 1867 = *Cythere minna* Baird, 1850, from the Recent, Shetland Islands.

Paracypris Sars, 1866 = *Paracypris polita* Sars, 1866, Recent, Norway.

Pedicythere Eager, 1965 = *Pedicythere tessae* Eager, 1965, pl. 2, fig. 6-8, London Clay (Lower Eocene) Reading, England.

Planileberis *C Deroo, 1966 = *Cythere lepida* Bosquet, 1854, pl.6, figs. 11a-d, Maastrichtian of Holland.

Pontocyprella *C Ljubimova, 1955 = *Cythere (Bairdia) harrisiana* Jones, 1849, p. 25, pl. 6, fig. 17a-f, Cretaceous of England.

Pterygocythere *C Hill, 1954 = *Cypridina alata* Bosquet, 1847, pl. 4, fig. 1a-d, Maastrichtian of Holland.

Pterygocythereis Blake, 1933 = *Cythereis jonesii* Baird, 1850, Recent North Atlantic.

Rehacythereis *C Gründel, 1973 = *Cythereis luermannae* Triebel, 1940, p. 201, pl. 6, fig. 63-66, Albian (*N. minimus* zone) of Hoheneggelsen bei Hildesheim, West Germany.

Saida Hornibrook, 1952 = *Saida truncala* Hornibrook, 1952, pl. 18, fig. 290-292 recent, New Zealand.

c) **By subsequent designation:**

Cytherella *C Jones, 1849 = *Cytherina ovata* Roemer, 1840, from the Campanian of western Germany.

Cythereis *C Jones, 1849 = *Cytherina ciliata* Reuss, 1846, p. 104, pl. 24, fig. 17, Turonian of Bohemia.

Eucytherura Muller, 1894, by subsequent designation Alexander, 1936 = *Cythere complexa* Brady, 1867, p. 210, recent, Hebrides.

Xestoleberis Sars, 1866, by subsequent designation, Brady & Norman, 1889 = *Cythere aurantia* Baird, 1838, from the Recent of Great Britain.

2 – Systematic taxonomy

Introduction.

Since the *Treatise* was published (*Treatise on Invertebrate Palaeontology, Part Q - Ostracoda.* Moore and Pitrat (eds) 1961), substantial increments to our knowledge of Cretaceous Ostracoda have taken place at specific, generic and supra-generic levels. As a consequence of this, it has become necessary to redefine and amend certain taxa, from family downwards. While certain families can be accommodated within the framework of their *Treatise* diagnosis, in other cases, these diagnoses are woefully inadequate, misleading or erroneous. Other genera were erected after 1961 and the generic diagnoses were taken from the original publication in which they first appeared. The emended diagnosis is similar to that which will appear in the *Treatise* revision and a database has been made freely available by the co-ordinating author of this revision. Some diagnoses, however, have been further modified due to the nature of the present fauna described in this thesis. [pers.comm. Prof. R. Whatley, January, 1999]

List of abbreviations used in the systematic taxonomy.

RV = right valve, LV = left valve, C = carapace, A = adult, Juv. = juvenile, RPC = radial pore canal, MPC = marginal pore canal.

Additional notes.

a) All illustrated specimens are curated under the catalogue numbers MPK 11272 - 11843 and have been deposited in the Museum of the British Geological Survey- Keyworth, Nottingham. A full list of catalogue numbers is included in appendix 5 of this thesis.

b) The following relative size conventions are employed:
"Very small" for specimens less than 0.40mm in length,
"Small" for specimens 0.40 to 0.50 mm in length,
"Medium" for specimens between 0.50 and 0.70 mm,
"Large" for specimens between 0.70 and 1.00 mm in length.
"Very large" for specimens greater than 1.00mm

c)The following prefixes are also used in the systematics

The prefix "cf." is used when a specimen is compared to a previously recorded species. e.g. *Cytherella sp. cf. C. parallela.*

The prefix "aff." is used when a specimen has an affinity with a previously recorded species, e.g. *Oertliella aff. pulchra* Babinot, 1980.

The prefix "gr." is applied when a specimen is a member of a group illustrating interspecific variation. e.g. *Bairdia gr. pseudoseptentrionalis.*

A total of 151 species, belonging to 53 genera, are encountered in this study and are treated taxonomically below. Of these, 18 species/subspecies are new. These are as follows: *Argilloecia argillos, Argilloecia cretula, Asciocythere hadratos, Asciocythere prionodes,, Eucythere ovoides, Eucythere sphenarion, Saida prasutegusi, Aversovalva apeorus, Semicytherura fasciculata, Cytheropteron cathetos, Sagmatocythere orthros, Schizocythere biponticulata, Mosaeleberis dictyotos, Mosaeleberis pseudomacropthalma Curfsina ceraunos, Cythereis campanianica, Cythereis ornatissima icenica, Phacorhabdotus leiodermatos.*

Fifty-three species have been described previously and a further 74 species have been left in open nomenclature due to either paucity, bad preservation or a combination of these two factors. In the case of six species, it has not been possible to determine their generic status. The upper part of the Upper Cretaceous in East Anglia has been little studied since Jones & Hinde's classic 1890 monograph and this thesis is the first major study since then. Jones & Hinde recorded only about 70 species . The present study, therefore, represents a more than two-fold increase in the known diversity of Ostracoda in these rocks. All the fauna belong to the Podocopida, with both Platycopina (8 species) and Podocopina (143 species) being represented. Of the Podocopina, seven species belong to the Cypridacea, eleven to the Bairdiacea and 125 to the Cytheracea.

The fauna is essentially similar to other European Upper Cretaceous Ostracod faunas in Chalk facies, but is closer to that of the French Northern Realm (as typified by the Paris Basin) and Northern Germany than to the Tethyan Realm (represented in France by Provence and Aquitaine). The reasons for this have already been discussed in Chapter 1

SYSTEMATIC DESCRIPTION.

Phylum CRUSTACEA Pennant, 1777
Class OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PLATYCOPINA Sars, 1866.
Family CYTHERELLIDAE Sars, 1866.

Genus CYTHERELLA Jones, 1849

Treatise reference. Q382

Treatise description of genus. "Carapace small to moderately large, thick shelled; surface smooth or ornamented with pits or ribs; RV larger than LV, its margin being grooved all around; shape and ornament of opposite valves commonly different. LV hinge with dorsal ridge, RV with corresponding furrow; no marginal pore canals, although normal canals in marginal area may resemble them."

Remarks. Jones (1849) originally proposed the genus as a subgenus of *Cythere* Müller, without designating a type species. Majoran (1989, p. 8) states that "one of the first problems one faces in dealing with an abundance of cytherellids, is to try and separate the different species. "Many other authors have commented on this in the past (e.g. Damotte, 1971a, Weaver, 1982). The valves are generally smooth and featureless, leaving only size and shape to serve as foundations for systematic classification. Separation based on shape and size is, however, of little use since each species shows a wide degree of variability and may be polymorphic (cf. Reyment, 1965, 1988. Ducasse, 1981, who carried out a "populationist study" of the genus *Cytherella* in the Palaeogene of the Aquitaine basin, recognised five species characterised by "important polymorphism and a stabilising evolution.") Damotte, 1971a, Weaver, 1982 and Majoran, 1989, 1990 carried out similar studies of Cretaceous representatives of the genus and report similar wide morphological variance. Individual species may be difficult to differentiate due to lack of surface features, differentiation between male and female dimorphs and phenotypical variation shown in specimens of the same species from different environments (Puckett, 1992). Four species are present in the material of this study; *C. ovata, C. cf. C. contracta contracta, C. parallela* and *C. cf. C. parallela.* Each species is relatively distinct from any other but show a wide range of valve shapes within its own species.

Cytherella cf. C. contracta contracta Van Veen, 1932

Pl. 1, fig. 16

cf.1932 *Cytherella contracta* Veen, p. 342, pl. 8, figs. 1-18

cf.1982 *Cytherella* aff. *C. contracta contracta* Veen. Weaver, p. 16, pl. 2, figs. 9-14.

Diagnosis. A medium, relatively thin-shelled species of *Cytherella;* elongate with narrow anterior marginal rim; anterior and posterior margins rounded, dorsal and ventral margins straight and parallel; lateral surface smooth.

Dimensions.	L	H
RV (MPK 11287)	0.55	0.27
LV (SAG 109, basal mucronata Chalk, Cringleford)	0.54	0.27
LV Juv? (SAG 109, basal mucronata Chalk, Cringleford)	0.50	0.23

Material. More than 30 specimens

Stratigraphical and Geographical range. Veen (1932) originally described the species from the Maastrichtian of South Limburg. Gründel (1969) described *C. contracta contracta* from the *Actinocamax plenus* zone of Germany, and Weaver (1982) illustrates the species from the Upper Cenomanian of Barrington, Cambridgeshire; Pitstone, Hertfordshire; Bluebell Hill, Kent; Glyndeboume, Sussex; Culver Cliff, Isle of Wight and several localities in Dorset.

Remarks. The material of the present study is identical to Weaver's specimens from the British Upper Cenomanian. It differs from Veen's original specimens and Gründel's *C. contracta contracta* (1966, p.

83, pl. 1, figs. 8, 9; 1970, pl. 1, figs. 5, 6) in being smaller and less high relative to length and a little wider in dorsal view. Weaver, 1982, had some doubts concerning the identity of his material, assigning the species *Cytherella aff. C. contracta contracta*. It is possible that the material of the present study may prove to be intermediate between the Maastrichtian and Cenomanian forms but, until this is proven, the suffix cf. is used. Majoran illustrated *Cytherella* aff. *contracta* from the Mid-Cretaceous of Algeria (1989, p. 8, pl. 1, figs. 9-10) but this is not considered by the present author to be conspecific with the present or Weaver's material. It is not, therefore, included in synonomy. Majoran's specimens are generally much larger (ranging from 0.59 to 0.64 mm in length). They are also less elongate, more heavily calcified and do not show the narrow anterior marginal rim seen in the present material. The species is very similar in shape to *C. parallela*, but differs in its smaller size, less heavily calcified valves and the narrow anterior marginal rim. It is also more elongate and is much less common in the material of the present study. It is also more restricted in terms of its appearance in the Trunch Borehole. Whereas *C. parallela* ranges from Lower Maastrichtian to Coniacian, *C.* cf. *C. contracta contracta* is restricted to Lower Maastrichtian to Lower Campanian strata, first appearing (FAD) in SAG 540 and then sporadically up into the Lower Maastrichtian to SAG 213. Weaver (1982, p. 14, pl. 1, figs 13-17; pl. 2, fig. 22) also describes a new species from the Upper Cenomanian of Kent; *C. concava* differs from *C. contracta* in its larger size and in the gently arched dorsal margin seen in the female RV specimens. In the latter species, both dorsal and ventral margins are straight and parallel to each other.

Range within present study. The species is never more than a rare component in any of the assemblages of the Trunch Borehole and is very rare in the outcrop samples. In the Trunch Borehole, it ranges from the Lower Campanian *Gonioteuthis quadrata* zone (First Appearance SAG 540) to the Lower Maastrichtian *Belemnitella lanceolata* zone (sample SAG 213). The presence of the species is, however, not continuous. Range, occurrence and abundance of the species is tabulated in Appendix 3; *C* cf *C. contracta contracta* appears as species 5

The species is also present in outcrop samples, but restricted to the Upper Campanian basal mucronata Chalk (Zone/subdivision 10) and Zone/subdivision 12 (Weybourne Chalk)

Cytherella ovata (Roemer, 1841)

Pl. 1, figs 1-8, 10, 11

1841 *Cytherina ovata* Roemer p.104, pl. 16, fig. 21.

1845 *Cytherina ovata* Roemer. Reuss, p. 16, pl.5, fig. 35.

1849 *Cythere (Cytherella) ovata* (Roemer). Jones, p.28, pl. 7, fig. 24 a-i.

1850 *Cytherella ovata* (Roemer). Reuss, p. 48, pl. 5, fig. 2.

1880 *Cytherella ovata* (Roemer). Marsson, p. 28.

1890 *Cytherella ovata* (Roemer). Jones & Hinde, pl. 3, fig. 48, 49.

non fig. 50 (= *C. truncata* - Bosquet)

1890 *Cytherella obovata* Jones & Hinde, p.46, pl. 4, fig. 39.
1929 *Cytherella ovata* (Roemer). Alexander, p. 47-48, pl. 1, fig. 1, 2.
1932 *Cytherella ovata* (Roemer). Alexander, pl. 28, figs 1-2
1932 *Cytherella navarroensis* Alexander, p. 53, pl. 2, figs 1, 2
1932 *Cytherella moremani* Van Veen. Alexander, p. 53, pl. 1, figs 4, 5
1956 *Cytherella ovata* (Roemer). Deroo, p. 1508, pl. 1, fig. 4-6.
1958 *Cytherella ovata* (Roemer). Howe & Laurencich, p. 251.
1958 *Cytherella ovata* (Roemer). Oertli, pl.1, fig. 10 - 29.
1965 *Cytherella ovata* (Roemer). Kaye & Barker, p. 385, pl. 50, fig. 10.
1965 *Cytherella ovata* (Roemer). Herrig, tab 2, fig. 13.
1966 *Cytherella ovata* (Roemer). Gründel, p.12, pl.1, fig. 2.
1966 *Cytherella ovata* (Roemer). Herrig, p. 718, text fig. 11-19; pl. 2, fig. 1-7.
1969 *Cytherella ovata* (Roemer). Gründel, pl. 1, fig. 1.
1971a *Cytherella ovata* (Roemer). Damotte, pl. 1, fig. 2-7.
1974 *Cytherella* gr. *C. ovata* (Roemer). Rosenfeld & Raab, p. 3, pl. 1, fig. 3-5.
1978 *Cytherella ovata* (Roemer). Neale, pg 333, pl. 1, fig. 1-2, tb.1.
1980 *Cytherella ovata* (Roemer). Babinot, pl. 1, fig. 12, pl. 2, fig. 1-3.
1980 *Cytherella* aff. *ovata* (Roemer). Babinot, pl. 1, fig. 13.
1982 *Cytherella* ex. gr. *C. ovata* (Roemer). Weaver, pl. 1, fig. 1-5; pl. 2, fig. 20.
1985 *Cytherella ovata* (Roemer). Robaszynski *et al.*, pl. 19, fig. 1-2.
1987 *Cytherella ovata* (Roemer). Babinot, Colin & Damotte, p. 244, pl. 55, fig. 1-2.
1989 *Cytherella ovata* (Roemer). Majoran, pl. 1, fig. 1-8.
1990 *Cytherella* cf. *C. ovata* (Roemer). Majoran, p. 41, pl. 1, fig. 1-12.
1991 *Cytherella* cf. *C. ovata* (Roemer). Swain *et al.*, p. 85, pl. 1, fig. 3,4.
1992 *Cytherella ovata* (Roemer). Witte *et al.*, pl. 1, fig. 8-10.
1997 *Cytherella ovata* (Roemer). Ismail & Soliman, p. 168, pl. 2, fig. 2, 3.
non. pl. 2, fig. 1.

Diagnosis. A relatively large species of *Cytherella*; carapace ovate in side view; greatest height slightly behind middle; dorsal margin arched, ventral margin convex; RV larger and overlaps LV, with the stongest overlap along the dorsal margin. Anterior and posterior margins rounded; anterior margin sub-acute, posterior roundly truncated. In dorsal view, the carapace is elongate-ovate.

Dimensions. A wide variance in length and height was seen in the specimens; a range of 0.90 to 0.30mm was not uncommon and a full ontogeny was preserved in most assemblages.

Material. at least 4000 specimens.

Remarks. The species is strongly dimorphic and exhibits a wide morphological variability in size and shape. Herrig, 1966, studied the population structure of this species in the Maastrichtian White Chalk of Germany using simple valve measurements. This study separated the assemblage into 9

ontogenetic stages. In 1971, Damotte, working on *C. ovata* from the Cretaceous Paris Basin, presented a series of length - height graphs drawn for the Albian, Turonian, Coniacian, Santonian and Campanian stages. This is discussed in further detail in chapter 4 of this thesis

Some specimens appear similar to *Cytherella* sp. 3 Colin, 1973, described by Babinot & Colin (1983, fig. 7a, p. 197) from the Late Cenomanian of the Dordogne, France. At least one other specimen appears similar to *Cytherella eosulcata* of Colin, 1974. Babinot & Colin describe this species from the Upper Turonian (1985, pl.55, fig. 7-9 (esp. fig. 9). It differs from the material of the present study in that the valves are very asymmetrical, the RV being more flattened than the LV and both valve with a longitudinal furrow. Jones & Hinde described *Cytherella obovata* from the "Chalk" of Kent. This is commonly assigned to the male of *C. ovata* (Alexander, 1932, p. 305) and the current author is in agreement. The material of this study also closely resemble Swain *et al.*, 1991 figured specimens of *Cytherella* cf. *C. ovata* but such specimens can easily be accomodated within the synonomy of *C. ovata* itself. In the systematic palaeontology (Swain *et al.*, 1991, p. 85), no explanation is given of why the suffix cf. is used. Although Damotte, 1971a, states that conspecific forms of *C. ovata* range from Aptian to Upper Campanian, with the range of this species being further extended by later authors, Weaver (1982, p. 12) prefers to regard the British Cenomanian forms as " belonging to a group of forms similar to *C. ovata* - hence the ex. gr. suffix. In the present study, Weaver's specimens are included in synonomy with *C. ovata* since the present author believes that the specimens belong to the same species. The material of the present study is identical to that of Ismail & Soliman (1997) from the Cenomanian to Turonian of Egypt, exept for fig. 1, which looks rather too inflated in dorsal view to belong in *C. ovata.*

In conclusion, there appears to be a great deal of confusion about this species, since the type specimens described by Roemer have long since been lost and a neotype has yet to be established. Topotype material was figured by Damotte (1971a, pl. 1, fig. 2, 3). It is clear, however, that specimens, even within individual samples, show a wide range of size and shapes. A full ontogeny is usually seen. Weaver also described the ontogeny (1982, text fig. 7,8, p. 13), which agreed in general with that of Maastrichtian specimens (e.g. Herrig, 1966, text fig. 11), although the British Cenomanian specimens are smaller. Gründel, 1966, demonstrates that size is a variable factor in adult specimens and this parameter should not be used in isolation to determine which specimens are assigned to *C. ovata* and which to *C. cf. C. ovata* when all other characteristics are identical. In the Lower Chalk, Weaver (p. 14) notes that "this species is most closely comparable to material described here as *Cytherella* cf. *C. truncata* (Bosquet) and *Cytherella medwayensis* sp. nov. The former can be distinguished by its truncate posteroventral margin in the right valve and by its relatively more elongate shape, particularly in left valves. *C. medwayensis* has a distinctly convex ventral margin in the right valve and is much more laterally compressed in dorsal view."

Stratigraphical and geographical distribution.

Neale, 1978, identifies it as " the most commonly recorded Cretaceous *Cytherella*" and states that the "true *Cytherella ovata* ranges from the Upper Aptian to Cenomanian" (pg. 333, 368) This range has been greatly extended by authors working in the Upper Cretaceous. Weaver (1982, p. 12) states that " *Cytherella ovata* s.l. is one of the most common and most recorded of Cretaceous ostracods in rocks of Aptian to Maastrichtian age, but it is probable that these occurrences represent more than one species."

Lower Cretaceous. Taylor and Navarro formations of Texas, Delaware and New Jersey, U.S.A (Alexander, 1929); Speeton Clay (Kaye, 1963);

Aptian. Upper Aptian - Sutterby Marl of South Lincolnshire (Kaye & Barker, 1965); Cambridge Greensand (Chapman, 1898); French Inferior Greensand (Damotte & Magniez-Jannin, 1973); Aptian of Florida (Swain *et al.*, 1991); Aptian to Albian of the Paris Basin (Damotte, 1963)

Albian. Late Albian, Fastnet Basin (Ainsworth *et al.,* 1987); Albian of France (Damotte, 1979); Aptian-Albian of Germany, Spain and Bulgaria (Damotte *et al.,* 1981); Middle Albian of Britain (Damotte, 1971); Aptian-Upper Albian of Lincolnshire (Neale, 1973); Hunstanton Chalk, Eastern England (Jones, 1849; Wilkinson, 1990); Lower Greensand and Gault of Folkestone; Flamborough Red Chalk; Lower Albian of France (Deroo, 1956); Albian of Florida (Swain *et al,* 1991)

Cenomanian to Turonian. Israel (Rosenfeld & Raab, 1974); Germany (Damotte *et al.*, 1981); plenus marls, Compton Bay, Isle of Wight (Johnson, 1996).

Turonian. Plenus zone- Lower- Upper Turonian, Saxony (Grundel, 1970); Upper Turonian, Germany (Grundel, 1969, 1970; Damotte *et al.*, 1981); Spain (Damotte *et al.,* 1981)

Albian to Cenomanian. Cambridgeshire and Suffolk (Wilkinson, 1988); France (Damotte & Grosdidier, 1963);

Cenomanian. Northern Germany; Northern Ireland (Keen & Siddiqui, 1971); Northeastern Algeria (Majoran, 1989, 1990); Dover Chalk Marl (Weaver, 1982); Lower Chalk of Bavaria and Northern Spain; Middle Cenomanian of Germany, Lower to Middle Cenomanian of Eastern Netherlands (Witte *et al.*, 1992);

Cenomanian to Santonian. Egypt, Horus Well - 1, Northwestern Desert (Ismail & Soliman, 1997).

Coniacian. South-Eastern France (Babinot & Tronchetti, 1983, p. 145)

Coniacian to Santonian. Gingin Chalk of Australia (Neale, 1975);

Santonian. Germany (Ohmert, 1973); France (Babinot, 1980);

Aptian to Cenomanian and Coniacian. Paris Basin (Damotte, 1971); Belgium; South-East France (Babinot & Tronchetti, 1983, p. 152, tab. 5);

Campanian. Upper Campanian- Paris Basin (Damotte, 1965; 1971a); Upper Campanian - Germany (Damotte, 1965, 1971a, Damotte et al., 1981);

Campanian to Maastrichtian. Type Maastrichtian area (Robaszynski *et al;* 1985; Lot *et al.,* 1985)

Cenomanian to Maastrichtian of the Paris Basin and Aquitaine; Cenomanian to Santonian of

Netherlands.

Range within this study. The species is very common, occurring in almost all samples, sometimes making up 50 to 75 % of the fauna (in several outcrop samples in the Santonian and early Lower Campanian it makes up 100% of component). It ranges from Santonian to Lower Maastrictian in the Trunch Borehole and Coniacian to Lower Maastrichtian in the outcrop samples. A full population study has been undertaken for this species and the results illustrated by a series of population histograms in chapter 3 of this thesis. Intervals of lowered oxygen levels can be identified from the increased platycopid numbers, *Cytherella ovata* being by far the most abundant species. A full ontogeny ranging from adult to the smallest juvenile instars was seen in most of the samples. The range, occurrence and abundance of the species is tabulated in Appendix 3. *Cytherella ovata* appears as species 1.

Cytherella parallela (Reuss, 1845)

Pl. 1, figs 9, 13-15.

1845 *Cytherina parallela* Reuss p. 76, pl. 5, fig. 33.
1849 *Cytherella truncata* (Reuss). Jones, p.30, pl. 7, fig. 25 a-e.
1854 *Cytherella parallela* (Reuss). Reuss, p.40.
1879 *Cytherella parallela* (Reuss). Brady, p. 407, pl. 62, fig 2a-c.
1880 *Cytherella munsteri* (Roemer). Marsson, p. 30.
1890 *Cytherella munsteri* (Roemer). Jones & Hinde, p. 46, pl. 3, fig. 63-67.
1929 *Cytherella parallela* (Reuss). Alexander, pl. 1, fig. 13, 16.
1940 *Cytherella parallela* (Reuss). Bonnema, p. 93, pl. 8, fig. 3a-b.
1963 *Cytherella parallela* (Reuss). Kaye, p. 111, pl. 18, fig. 1-6.
1966 *Cytherella parallela* (Reuss). Gründel, p. 12, pl. 1, fig. 4,
1966 *Cytherella parallela* (Reuss). Herrig, p.728, pl.3, fig. 1, 2, 4.
1971 *Cytherella parallela* (Reuss). Damotte, pl. 1, fig. 8.
1974 *Cytherella parallela* (Reuss). Rosenfeld & Raab, p.3, pl. 1, fig. 1-2.
1980 *Cytherella* cf. sp. *C. parallela* (Reuss). Babinot, pl. 2, fig. 4-5.
1983 *Cytherella cf. parallela* (Reuss). Babinot & Tronchetti, p. 143.
1985 *Cytherella parallela* (Reuss). Babinot *et al*, pl.55, fig. 10.
1985 *Cytherella* gr. *parallela* (Reuss). Viviere, pl. 1, fig. 2.

Diagnosis. Dorsal and ventral margins straight and parallel; anterior and posterior margins rounded, posterior margin slightly narrower than anterior margin. Surface smooth; RV overlaps LV around entire margin. Carapace subovate in side view; widens posteriorly in dorsal view; anterior end acute; posterior roundly truncated.

Dimensions.	L	H
RV (MPK 11283)	0.67	0.40

LV (MPK 11282)	0.67	0.39
C (MPK 11284)	0.69	0.40
LV Juv. (MPK 11285)	0.63	0.37
LV A-1 Juv (SAG 109)	0.60	0.33

Material. more than 1000 specimens

Remarks. This species differs from *C. ovata*, in that it is parallel-sided rather than oval. *Cytherella contracta contracta* Van Veen is similar in shape. However, the anterior and posterior margins of this species appear to be less rounded than the specimens assigned to *C. parallela*. It is also smaller and less heavily calcified.

Stratigraphical record and geographical distribution.

Babinot *et al.*, 1985, note that *C. parallela* is a well-documented species throughout the European Cretaceous, especially in Aptian to Maastrichtian assemblages.

Aptian. Upper Aptian of Provence, France (Damotte, 1971a); Aptian to Upper Albian of Lincolnshire and Yorkshire (Neale, 1973); Aptian of Northern Germany (Andreu, 1983).

Albian. France (Damotte & Grosdidier, 1963; Damotte, 1963,1979); Late Albian of Fastnet Basin (Ainsworth *et al.*, 1987); Middle Albian of Britain (Damotte, 1971a); Hunstanton Chalk of Eastern England (Wilkinson, 1990).

Aptian / Albian to Cenomanian. Aptian to Cenomanian of Paris Basin; Albian to Cenomanian of Germany (Damotte, 1971); Albian to Cenomanian of Cambridgeshire and Suffolk, England (Wilkinson, 1988b).

Cenomanian to Turonian. Germany (Damotte, 1971a, Herrig, 1966, Gründel, 1966, 1970); Israel (Rosenfeld & Raab, 1974).

Coniacian. Lower Coniacian, France (Damotte, 1971; Babinot *et al.*, 1985);

Cenomanian to Santonian. France (Babinot *et al.*, 1985); Egypt (Ismail & Soliman, 1997)

Coniacian - Santonian. South-eastern France (Babinot & Tronchetti, 1983)

Santonian. North-eastern Algeria (Viviere, 1985)

Campanian. Upper Campanian - Paris Basin (Damotte, 1965, 1971)

Cenomanian to Maastrichtian. Paris Basin and Aquitaine (Babinot, *et al.*, 1985)

Maastrichtian. Germany (Herrig, 1966); South Pyrenees (Liebau, 1984);

"Upper Cretaceous". Exact age not given - Northern Texas (Alexander, 1929); Provence, France (Babinot, 1980); Czechoslovakia.

Range within this study. The species is common in the Trunch Borehole and outcrop samples, ranging from Santonian to Lower Maastrichtian (Trunch Borehole, SAG 630 to SAG 213).

Cytherella cf. *C. parallela* (Reuss, 1845)

Pl. 1, fig. 12

Material. A single specimen.

Depository. MPK 11286

Remarks. Identical in size and shape to *C. parallela,* differing only in the slight ornament seen in the posterior half of the valve. Left without firm designation due to its rarity but it is probably synonymous with the aforementioned species

Dimensions. MPK 11286: L= 0.67 mm, H= 0.40 mm..

Range within study. A single specimen was retrieved from the upper Upper Campanian, Beeston Chalk of Caistor St. Edmund, Norfolk (SAG 57).

Genus CYTHERELLOIDEA Alexander, 1929.

Treatise reference: p. Q382- 383.

Treatise description of genus. " Differs from *Cytherella* in generally stronger ornament, especially ribbing, and generally more compressed shell form; variation within a single species may range from strongly ornamented to entirely smooth,"

Remarks. Adult females of the genus show two posterior internal brood pouches in each valve while, in the genus *Cytherella,* there is only one such chamber. This is an important diagnostic tool by which the two genera may be differentiated. The genus *Platella* Coryell & Fields, 1937, shows a similar shape to *Cytherelloidea,* with female specimens showing two posterior brood pouches, but the valves are weakly calcified, ornamented with a series of external pits and generally lack ribs. Although Van Morkhoven considered Coryell & Fields' genus to be synonomous with *Cytherella* on the basis of its shape, more recent authors (e.g. Bate, 1972, Colin, 1974) finding more sub-rectangular, pitted forms have retained *Platella* as a separate genus. Weaver, 1982, p. 24, describes a new species from the British Cenomanian. It is entirely feasible that Cretaceous assemblages may contain representatives of both *Cytherelloidea* and *Platella* but there would be no difficulty in distinguishing between the two.

Alexander (1929, p. 9) erected the genus *Cytherelloidea* to receive a number of forms, fossil and recent, previously regarded as members of *Cytherella* Jones, but which differ in many respects from the original generic description. The type species is *Cytherella williamsoniana* Jones. There appears, however, to be some confusion surrounding this species. Jones (1849) appears to have regarded all the specimens of *Cytherella* with ribs as belonging to *C. williamsoniana* and figures what are now regarded as three distinct species; *C. stricta* (Jones & Hinde, 1890), *C. parawilliamsoniana* Kaye, 1963a and *C. williamsoniana* (Jones) (see also Kaye, 1964; Weaver, 1982, p. 19). Jones' figure 26f, from the Chalk of Gravesend may be taken as typical and was proposed as a lectotype for *C. williamsoniana* by Howe & Laurencich, 1958. Weaver, however, notes that "the specimen relating to this figure were lost long before 1958 and consequently the species is a *nomen dubium* being restricted to a single figure without specimens."

Alexander (p. 55) also gives a full generic description and notes that the hinge, as in *Cytherella,* consists of a groove in the right valve and a flange in the left. The genus is described as " oblong-ovate or sub-quadrangular; carapace compressed, especially in front; greatest width at posterior. The two

valves are subequal, the right valve being slightly larger than the left, and never overlapping it strongly or extending beyond it for more than a short distance along the periphery. Surface always more or less sculptured, bearing tubercles, ridges and pits and usually with a narrow, convex, marginal ridge extending around the periphery of the valves." Van Morkhoven (1962, p. 221-23) notes that although *Cytherelloidea* differs from *Cytherella* by the presence of a clear ornamentation, "transitional forms occur with a varyingly pronounced punctation of the lateral surface." Strongly ribbed, puncatate forms may pass through transitional stages into nearly smooth forms, which are more like *Cytherella*. An example of this can be seen in Van Morkhoven's figure 28 (1962, p. 40) which shows the gradual morphogenetic changes in the ornament of *Cytherelloidea ovata* Weber in the Lower Cretaceous of northwestern Germany. Wilkinson (1988 MS, text figure IV-2) shows the evolutionary relationships in the genus during the Upper Jurassic and Lower Cretaceous of Northwestern Europe. In the Hauterivian, Barremian to Albian, the eleven species are all strongly ribbed and heavily ornamented. In the Cenomanian, species such as *C. globosa, C. kayei* and *C. stricta* have evolved from these earlier ornate forms to show a mostly smooth lateral surface which is broken only by an anterior and ventral rib.

Palaeoecological note on *Cytherelloidea.*

Sohn (1964) makes the point that this genus is thermophylic and will not occur at depths greater than 100 metres (see also Whatley *et al.*, 1994), even in the tropics. At the present day, the distribution of the genus *Cytherelloidea* is "bounded roughly by Lat. 40 ^{o}S and Lat. 30^{o}N and also by the 10^{o}C Isocrym." Isocryms are isotherms (lines connecting equal temperatures) which connect points that cool down to the same extremes when measured in monthly mean temperature. Temperature is probably a major factor in controlling the distribution of living species of the genus (Sohn, 1962 a, 1964). Assuming that the genus did not adapt over time to a different minimum temperature zone, the distribution of fossil species should give a relative palaeotemperature. Samples with abundant *Cytherelloidea* are generally assumed to have lived in warmer waters than those samples in which *Cytherelloidea* is absent or rare. This is the assumption followed in this study. Van Morkhoven (1962, p. 21-23) gives a warm shallow water habitat for this genus, in keeping with most subsequent authors.

It should, however, be noted that Johnson (1993, 1996, 1997a, 1997b and 1997c) states that the "virtual absence of *Cytherelloidea* from English sections during the Cenomanian-Turonian, and a detailed study of the global palaeobiogeography of this genus may, in conclusion, challenge the widely accepted view that it is an indicator of warm waters." Few authors have supported this theory as yet and the general assumption remains valid.

Wilkinson (1988b, p. 1238) gives some detail about the earlier Cretaceous history of East Anglia prior to the Coniacian. "During much of the Late Albian in Eastern England, deposition of the Gault and Hunstanton Chalk took place in quiet, shallow but gradually deepening marine conditions. The rapid transgression that took place in the Early Cenomanian resulted in the Cambridge Greensand facies, rapidly passing up into the Chalk Marl. Water temperatures also increased with the transgressive regimes, warmer water entering the area from the South when the Anglo-Paris Basin was widened. It increased slowly through the Upper Albian, but it was not until after the 'Mid-Cenomanian Break' that major temperature increases took place." Prevailing conditions during the Coniacian to Lower Maastrichtian can be assumed to have been similar to those during the topmost late Albian to Cenomanian, i. e. quiet and relatively shallow. Slight temperature fluctuations may be determined by the warm water marker genus *Cytherelloidea,* based on Sohn's 1964 temperature and depth limits. Wilkinson makes no mention of the genus in this context, but an examination of text fig. 3 (p. 1235) shows that 4 species were found. The Gault interval contained 0 to 1 species. The Cambridge Greensand and Chalk Marls assumed to be deposited in warmer waters than the Gault, commonly contained 2 of the 4 representative species.

Bless (1988, p. 60-61), in an examination of Upper Campanian lithofacies and ostracod assemblages in South Limburg and North-eastern Belgium, states that the genus *may* be important for a palaeoecological interpretation of the White Chalk facies. The composition of ostracod assemblages in this area is "clearly facies controlled". Environmental conditions differed during deposition of the almost pure coccolith ooze of the Chalk and that of the glauconitic marl facies. *Cytherelloidea* is one of the genera, which characterise the facies of the White Chalk. In the area of study (Antwerp - Aachen area; Bless, 1988, p. 59), this genus displays a distinct maximum in relative frequency, abundance and diversity in the Upper Campanian White Chalk, with six species recorded. Bless states that the fact that the genus is practically restricted to the White Chalk "matches observations on recent *Cytherelloidea* which prefer a muddy substrate and avoid sandy bottoms, hardgrounds and substrates colonised by algae.

King (1968 MS, pp. 29-37) discusses the genus and notes a striking discrepancy in the relative abundance of the sexes. No males of *C. hindei* were recorded in the 1968 study (out of 74 specimens). For *C. granulosa*, the percentages of males were as follows: "43.5% out of 131 specimens for horizons below the Catton Sponge Beds; 34% out of 240 specimens from the Catton Sponge Beds and Beeston Chalk; 36.1% out of 130 specimens from the *Porosphaera* Beds and Sponge Beds, and 39.5% out of 91 specimens from the Maastrichtian White Chalk" = *O. lunata* Chalk. In nearly all 11 species of *Cytherelloidea,* males are less abundant than females, the exception being represented by small numbers of specimens (see King, p. 34; Triebel, 1941, p. 356). This trend was seen in the present study in at least two species (*C. granulosa* and *C. hindei*).

Males were relatively poorly represented but easily distinguished from the females by their more elongate and less inflated carapaces.

1880 *Cytherelloidea granulosa* (Jones). *Cytherella williamsonia bosqueti* Marsson, pl. 2, fig 8d-e.
1890 Cytherella *williamsonia granulosa* (Jones). Jones & Hinde, p.49, fig. 69-72.
1929 *Cytherelloidea granulosa (*Jones). Alexander, p. 57, pl. 2, fig. 7.
1940 *Cytherelloidea williamsoniana* (Jones). Bonnema, p. 95, pl. 1, fig. 44-47.
1958 *Cytherelloidea granulosa* (Jones). Howe & Laurencich, p.265.
1958 *Cytherelloidea bosqueti* (Marsson). Howe & Laurencich, p.261.
1964 *Cytherelloidea granulosa* (Jones). Kaye, pg. 71-72, pl. 9, fig. 24-26.
1965 *Cytherelloidea granulosa* (Jones). Damotte, pl. 4, fig. 9.
1966 *Cytherelloidea granulosa* (Jones). Herrig, p. 750, pl. 6, figs 7-9; pl. 7, figs 2-9.
1968 *Cytherelloidea granulosa* (Jones). King, MS, p. 48, pl. 1, figs 1-5.
1971a *Cytherelloidea granulosa* (Jones). Damotte, pl. 1, fig. 4; pl. 6, fig. 9.
1978 *Cytherelloidea granulosa* (Jones). Neale, p. 358, pl. 13, fig. 12 - 13, table 5.
1987 *Cytherelloidea granulosa* (Jones). Babinot *et al.*, p. 223, pl. 55, fig. 12-13.
1988 *Cytherelloidea granulosa* (Jones). Bless, p. 63, text fig. 6d, pl. 2, fig. 9.
1990 *Cytherelloidea granulosa* (Jones). Horne *et al.*, p. 127, pl. 2, fig. 2.
1997 *Cytherelloidea granulosa* (Jones). Slipper, pl. 3, figs 5, 6, 8; pl. 4, fig. 1.
1997 *Cytherelloidea granulosa* (Jones) *parca.* Slipper, pl. 4, fig. 2, 3.

Diagnosis. A large, easily identifiable species of *Cytherelloidea,* distinguished by its pustulose surface comprising many rounded tubercles of variable size and abundance. It has a marked anterior marginal rib; short separate dorsal and longitudinal ribs; no median rib; dorsal margin straight or gently arched; ventral margins slightly sinuous. Anterior and posterior margins rounded. Posterior brood pouches in the adult female are particularly well developed and inflated.

Dimensions.	L	H
LV male (MPK 11293)	0.84	0.50
RV female (MPK 11288)	0.78	0.46
RV female (MPK 11289)	0.80	0.48
RV female (MPK 11290)	O.77	0.42
RV female (MPK 11291)	0.75	0.42
LV Juv. A1 (MPK 11292)	0.71	0.40
Juv. A2 (SAG 53, Beeston Chalk)	0.67	0.35
Juv. A3 (SAG 53, Beeston Chalk)	0.60	0.25

Material: Over 1000 specimens.

Remarks: This species, originally described as a variety of *C. williamsoniana* by Jones (1849), is characteristic of the Upper Chalk. Neale (1978) figures specimens from the Upper Chalk of Norwich and these specimens appear very similar to those of the present study. Howe and Laurencich's specimens also came from the Chalk at Thorpe, near Norwich. The specimens of this study, especially those from the Trunch Borehole, come from the same area and such a similarity is to be expected. Kaye (1964)

considers Marsson's *C. williamsonia var. bosqueti* to be conspecific with *C. granulosa*. Herrig, 1966, lists both species as present in the White Chalk of Rügen, and the two species, as figured in Herrig's plates, appear to be very similar in size, shape and ornamentation. King (MS, 1968) illustrates specimens that are identical to the present material. He notes that "specimens from the Upper

The specimens in this study normally show stronger pustulation than those figured by Bless (1988) from the Upper Campanian of Southern Belgium. It should be noted that *C. granulosa* shows a wide variation in the degree of ornamentation in adult and juvenile specimens. The size, clarity and number of the tubercles varied greatly, as can be seen in plate 1, figs 17-21. There is also a marked sexual dimorphism but females are significantly more abundant. Adult males are always more elongated than the females and appear narrower in dorsal view. Adult females are generally more inflated and have two posterior brood pouches. A full ontogeny is seen in the assemblages of the Trunch Borehole, ranging from adults of both sexes to juvenile stages (at least A4, possibly A5). Juveniles are distinguishable from adult specimens, usually the ribbing is subdued but the strong pustulation is evident at an early stage of development. Valves are usually disarticulated, due to the simple articulation of the adont hinge but, in some samples, complete carapaces may form a moderate percentage of the *C. granulosa* component. Slipper (1997 MS; erects a new subspecies (*C. granulosa parca*) from the Upper Turonian of Dover. This looks very similar to *C. granulosa* of other authors and the present material. Since Slipper's subspecies appears in an unpublished manuscript, with no validity for the purposes of nomenclature, it is here included in synonymy with Jones' original species.

Stratigraphical and geographical distribution.

The stratigraphical range of this species is well documented in the higher British Chalk. It is abundant in the Upper Campanian and Maastrichtian, common in the Santonian but rather rare below that horizon (Neale, 1978). Neale notes that it is extremely abundant in the Upper Campanian and Lower Maastrichtian, but is also common down to the *coranguinum* Zone. King (1968, MS) had recorded it from as low as the plenus zone (Cenomanian). Kaye (1964) has not found the species below the *Micraster coranguinum* zone.

"Upper Cretaceous". Chalk of Norwich and County Antrim, Northern Ireland (Jones, 1849; Jones and Hinde, 1890)

Albian. Northern Texas (Alexander, 1929); Gault of Folkestone;

Upper Campanian. Paris Basin (Damotte, 1965, 1971; Babinot *et al.*, 1983, 1985, 1987); Southern Belgium, South Limburg and Northeast Limburg (Bless, 1988); British Chalk (Neale, 1978)

Lower Maastrichtian. White Chalk, Germany (Herrig, 1966); British Chalk (Neale, 1978);

Range of species in this study. In the Trunch Borehole, this species ranges from the basal Lower Campanian (FAD = SAG 602) to upper Upper Campanian, disappearing just below the Campanian - Maastrichtian boundary (LAD = SAG 267, reaching its maximum abundance immediately below this interval (19 % of the assemblage of SAG 277 made up of *C. granulosa*). Range, occurrence and abundance of the species is tabulated in Appendix 3. *C. granulosa* appears as species 5. In the outcrop

localities, the species ranges from the Coniacian coranguinum Zone to the Lower Maastrichtian Grey Beds. It is a Lazarus taxa in the Santonian of East Anglia, but was found in comparative samples from the Santonian high *coranguinum* Zone (Witham and Kelvedon Boreholes) of Essex. In East Anglia, the species appears again in the upper part of the *pilula*/restricted *quadrata* Zone (8), but is more common in the restricted *quadrata* Zone (9). It is significantly more abundant in the Upper Campanian, where it often appears ubiquitous in the samples from the basal mucronata (10) to the upper Paramoudra Chalk (subdivision 14). It is most abundant in the Beeston Chalk (13) of Caistor St Edmund and West Runton, reaching maximum abundances of 38-45%. The species is present throughout the Lower Maastrichtian pre-*Porosphaera* (15) *Porosphaera* (16), *O. lunata* Chalk (17) and Grey Beds (18) of Trimingham and Sidestrand. No representatives of the genus were seen in the Lower Maastrichtian samples of the Trunch Borehole. Since *Cytherelloidea* is a proven thermophilic genus and a warm water indicator, it is possible that the absence of species of *Cytherelloidea* above the Campanian-Maastrichtian boundary may indicate a localised cooling event. In the outcrop samples, the genus persists into the Lower Maastrichtian of Sidestrand and Trimingham (north Norfolk) and is in some samples relatively abundant and diverse. This may suggest that water temperatures in Norfolk during the Lower Maastrichtian were warmer in the northern part of the basin than in the Southern part. It may, however, be due to water depth. The genus is restricted to the upper 100m; an absence in one area may simply reflect a localised deepening event.

Cytherelloidea hindei Kaye, 1964.

Pl. 2, figs 2-5, 11.

1964a *Cytherelloidea hindei* Kaye, pl. 3, fig. 13-16

1964b *Cytherelloidea hindei* Kaye, p. 72, pl. 9, fig. 4, 8, 11.

1965 *Cytherelloidea mariei* Damotte, p. 236, pl. 1, fig. 7a-d.

1968 *Cytherelloidea hindei* Kaye. King, MS, pl. 2, figs 3, 4.

1971a *Cytherelloidea hindei* Kaye. Damotte, p. 57, pl. 1, fig. 13.

1978 *Cytherelloidea hindei* Kaye. Neale, p. 358, pl. 13, fig. 5, table 5.

1982 *Cytherelloidea hindei* Kaye. Weaver, p. 22, pl. 3, fig. 13-16.

1982 *Cytherelloidea hindei* Kaye. Clarke, p. 49, pl. 2, fig. 3.

1988 *Cytherelloidea hindei* Kaye. Jarvis *et al.*, p. 34, fig. 15f.

1988 *Cytherelloidea* sp. cf. *C. chathamensis* Weaver, 1982. Jarvis et al., p. 34, fig. 15b.

1990 *Cytherelloidea hindei* Kaye. Horne *et al.*, p. 127, pl. 2, fig. 2.

1996 *Platella* sp., Slipper, p. 52, pl. 1, fig. 1.

1997 *Cytherelloidea hindei* Kaye. Slipper, MS, pl. 4, figs 4-8.

Diagnosis. A medium sized species in which the anterior marginal rib, ventral longitudinal rib and sinuous dorsal longitudinal rib are all connected; ventral rib and ventral margin coincide in lateral view;

concave upward median rib not connected to any other rib; intercostal areas smooth.

Dimensions.	L	H
LV male (MPK 11294)	0.68	0.32
RV male (MPK 11295)	0.68	0.30
LV male (MPK 11296)	0.66	0.30
RV female (MPK 11297)	0.63	0.34
RV female (MPK 11298)	0.61	0.35

Material. More than 100 specimens

Remarks. Neale's figured specimens come from the Upper Chalk of Norwich, as well as those of Kaye, 1964 (Holotype, BM Io 1288, right valve, figured by Kaye, 1964a, pl. 9, figs. 4, 11); both are very similar to the specimens of the present study. In 1965, Damotte described a species from the Paris Basin of France, *C. mariei,* which is accepted as a junior synonym of *C. hindei* (Damotte, 1971, p. 58). Weaver found the species in the British Cenomanian and notes a minor difference in morphology. Such specimens have a more pronounced anterior and dorsal shelf in the RV compared to Upper Chalk material, but are otherwise identical. *C. hindei* is easily distinguished from any other Cretaceous species; diagnostic features are as follows " lateral surface bounded by a continuous rib formed by the combination of a high straight ventral rib, a sinuous dorsal rib and a gently curved, high posterior rib." (Weaver,1982, p.22). The present author agrees with Slipper (1997, MS) in including *Platella* sp. (Slipper, 1996) in synonymy with *C. hindei*, the former identified as juvenile stages of the latter.

Stratigraphical Range and Geographical Distribution.

C. hindei is recorded from the British Santonian and Campanian (Kaye, 1964; Neale, 1978). It also occurs in the same interval in the French Paris Basin (Babinot *et al.,* 1983). In the Paris Basin, Damotte (1971a) gives a range of Lower Campanian (*Actinocamax quadratus* zone) to basal Upper Campanian (*Belemnitella mucronata* zone). King (1968, MS), in a study of selected British Upper Chalk Ostracoda gives a range of *coranguinum* Zone (Coniacian) to *mucronata* Zone (Upper Campanian). Hilbrecht *et al.,* 1996, record the species from the Cenomanian to Turonian of Southern Germany, but do not illustrate specimens. The range can be extended in Britain from both Kaye and Neale's published range of Santonian to Campanian by reference to Weaver (1982) and Johnson (1996) who both record the species from the British plenus marls.

Range within this study. In the Trunch Borehole, *C. hindei* ranges from the Lower Campanian (FAD = SAG 584) to the uppermost Upper Campanian (LAD = SAG 286). In the outcrops, the species ranges from the Coniacian to Lower Maastrichtian. It first appears in the Coniacian basal *coranguinum* Zone (1) through the low *coranguinum* (2) and *coranguinum* (3) Zone in both Norfolk and Suffolk. It is also present in the Santonian high *coranguinum* Zone (4) at Stowlangtoft, Suffolk. It was found in the corresponding Witham and Kelvedon Borehole samples from Essex (SAG 2057, 2058). It reappears in East Anglia in the top sample of the Lower Campanian *pilula* Zone (7) and the top 2 samples of the *pilula*/restricted *quadrata* Zone (8), but is more abundant in the Upper Campanian (zones 10-14; basal

Cytherelloidea obliquirugata (Jones & Hinde, 1890)

Pl. 2, figs 6-9.

1890 *Cytherella obliquirugata* Jones & Hinde, p. 50, pl. 3, fig. 73.

1929 *Cytherelloidea obliquirugata* (Jones & Hinde). Alexander, p. 58, pl. 2, fig. 8.

1958 *Cytherelloidea obliquirugata* (Jones & Hinde). Howe & Laurencich, p. 266-267.

1963 *Cytherelloidea obliquirugata* (Jones & Hinde). Coryell, p. 770.

1964 *Cytherelloidea obliquirugata* (Jones & Hinde). Kaye, p. 73, pl. 9, fig. 12, 14.

1968 *Cytherelloidea auricularis* Bosquet. King, MS, p. 39, pl. 3, figs 4-9.

1978 *Cytherelloidea obliquirugata* (Jones & Hinde). Neale, p. 358, pl. 13, fig. 3-4.

1985 *Cytherelloidea obliquirugata* (Jones & Hinde). Robaszynski *et al.*, fig. 19, fig. 1.

1988 *Cytherelloidea obliquirugata* (Jones & Hinde). Bless, text fig. 6d, pl. 2, fig. m.

1997 *Cytherelloidea obliquirugata* (Jones & Hinde). Slipper, MS, pl. 5, fig 4-6.

Diagnosis. A medium, ovate to ovate-oblong species with a sinuous dorsal rib and well developed ventral rib, generally with posterior noding. The median rib curves up to join the dorsal rib posteriorly; dorsal margin straight or slightly sinuate; anterior margin broadly rounded; posterior margin narrower and obliquely rounded. The anterior margin has a narrow peripheral rim, surface with several obliquely parallel costae and a small sub-central pit.

Dimensions.

	L	H
RV female (MPK 11299)	0.65	0.36
LV male (MPK 11300)	0.72	0.32
RV male (MPK 11301)	0.75	0.32
RV female (MPK 11302)	0.67	0.35

Material. More than 20 specimens

Remarks. Neale's figured specimens come from the Upper Chalk of Norwich, as do those of Kaye. The material of the present study appear very similar to the specimens of both authors. King (1968, MS) considers *C. auricularis* of Bosquet (1847) to be the correct name for this species but to maintain the *status quo* and follow most other workers, this study retains *C. obliquirugata*. Throughout the ontogeny of this species, the median longitudinal rib becomes less prominent. The ventral rib is also more strongly joined than in related forms, particularly in the males and juveniles. This feature can clearly be seen in Kaye, 1964 (pl. 9, figs 12-14), Neale's figured specimens, the material illustrated by Slipper (1997, MS) and in the present study. Slipper, writing on *C. auricularis*, notes that "juvenile *C. oblinquirugata* resemble *C. auricularis* in adult form but latter has a greater convexity and concavity in dorsal and ventral margins respectively".

Stratigraphical range and geographical distribution. The species ranges from Upper Turonian (*plenus* zone) to the Lower Maastrichtian in the British Chalk. King (1968, MS) agrees with this range but notes that the majority of his specimens were from the Upper Campanian. The species is also known from

Holland, Belgium and the German White Chalk (Herrig, 1966). Alexander, 1929, lists it in the Lower Cretaceous Grayson Formation and Upper Albian of Texas. Bless, 1988, records it from the Upper Campanian of South Limburg and Northeastern Belgium.

Range of species in present study. The species is rare in the Trunch Borehole, with a relatively short, sporadic range (FAD = SAG 504, LAD 308), ranging from the upper Lower Campanian to the lowest part of the Upper Campanian Paramoudra Chalk. The range, occurrence and abundance of the species is tabulated in appendix 3; *C. obliquirugata* appears as species 8. The species is also rare in the outcrop samples (range Upper Santonian to Lower Maastrichtian), but is slightly more common in the Beeston Chalk of Caistor St. Edmund.

Cytherelloidea sp.

Pl. 2, fig. 10

Diagnosis. A distinctively ornamented species; anterior margin broadly rounded with distinct marginal rim which shows at least 4 thin lines extending parallel to the margin; dorsal margin sinuous; ventral margin almost straight with curving ventral rib which is parallel and situated below a similar median rib. Posterior margin also broadly rounded but does not show clear brood pouches, so that specimen is either a male or a late stage juvenile female; ornament consists of a regular network of hexagonal polygons covering much of the lateral surface.

Dimensions.	L	H
LV (MPK 11303)	0.69	0.27

Material. A single LV specimen

Remarks. The specimen is relatively well preserved and the ornament is distinct from any other species seen in the literature. It is a similar shape to *C. granulosa* but is more elongate and less high; differing in the ornament and position of the median and ventral ribs. It is quite similar to *C. cf. rehburgensis* Bartenstein & Brand, as illustrated by Lott *et al.*, 1986, from the Speeton Clay Formation in the southern North Sea Basin. The ventral and median ribs are identical but the anterior rib is broader and more pronounced in cf. *rehburgensis* and the hexagonal polygons of the ornament are deeper. *Cytherelloidea ovata* of Weber, 1934, also illustrated by Neale in 1978 from the Speeton Clay, is similar in shape and nature of the ribs, but is a larger species and differs in ornament. *C. stricta* (Jones and Hinde, 1890) has a similar pattern of lines on the anterior marginal rim; the ornament is also rather similar to that of *Cytherelloidea* sp. of this study. However, when *C. stricta*, as figured by Wilkinson (1988a, ms., pl.1, fig. 10) is compared with the present material, several differences can be seen: the former is more elongate, narrower; the ventral rib is convex rather than straight. *Cytherelloidea sp.* is probably new but must be left in open nomenclature due to its rarity.

Range within this study: restricted to a single specimen present in the Upper Campanian of the Trunch Borehole, Norfolk (SAG 308).

Suborder PODOCOPA Sars, 1866,

Superfamily BAIRDIACEA Sars, 1888

Family BAIRDIIDAE Sars, 1888

Subfamily BAIRDIINAE Sars, 1888.

Genus BAIRDOPPILATA Coryell, Sample & Jennings, 1935.

Treatise reference. Q 205

Treatise diagnosis. "Like *Bairdia* but each valve with short series of transverse teeth and sockets in antero- and posterodorsal positions, in selvage of RV and selvage groove of LV. *L. Cret. - Tert.*"

This range has now been extended and Recent species are well-documented. A better generic diagnosis is that of Weaver, 1982 (p. 24): " Outline ovate to subtrapezoid, dorsal margin strongly arched in larger LV. Anterodorsal and posterodorsal margins straight to concave. Hinge with auxiliary dentition at anterior and posterior marginal angles consisting of several small denticles."

Taxonomic note. Sohn (1958, p. 1646; also Kornicker, 1961) restricts the stratigraphical range of *Bairdia (sensu stricto)* to the Middle Devonian to Permian, stating that "additional genera can, and should, be erected for post-Paleozoic species currently referred to *Bairdia*. Criteria for separating the groups are carapace shape, hingement, denticulate margins, presence of ventro-terminal loculae, combined with the soft-part anatomy of living species." The genus *Bairdoppilata*, based on the Lower Miocene type species *B. martyni* was distinguished from *Bairdia* McCoy, 1844, by the "articulating pattern that includes the transverse teeth - a feature now known as Bairdoppilatan Structures" (Pokorny, 1977, p. 345). Recent species were attributed to *Bairdoppilata*, as were all post-Palaeozoic species (Kornicker, 1961; Maddocks, 1969; Titterton & Whatley, 1988). Damotte, 1971a (p. 48) discusses *Bairdia* and *Bairdoppilata* and explains why, in her systematic taxonomy, species continue to be referred to the former genus.

Van Morkhoven, writing in 1963 (p. 34) states that "*Bairdoppilata* was erected for those *Bairdia* species in which a number of small denticles (in RV) and sockets (in LV) are present in the anterior and posterior marginal angles of the valves. They are too far removed from the hinge line to form part of the hinge mechanism. Their exact purpose is as yet unknown. As similar denticles in *Triebelina* species would not seem to constitute a generically constant feature, and moreover, since it is not known whether they may also be present in the Carboniferous type species of *Bairdia*, it is considered desirable to regard *Bairdoppilata* as synonymous with *Bairdia*." Most recent authors disagree.

Pokorny (1975a, 1975b, 1976, 1977, 1980) documented the genus from the Upper Cretaceous of Czechoslovakia. He discusses why post-Palaeozoic representatives of the sub-family Bairdiinae can be "problematic" (1975b, p. 321). Many of the species are similar, most have more or less smooth carapaces with relatively few diagnostic characteristics and the valves vary in their outline. This variability is further complicated by the fact that their sexual dimorphism is not strong enough to allow clear discrimination between sexes in any one species. Pokorny (ibid.) notes that "a biologically meaningful statistical evaluation of biometric data is much limited."

Due to the close similarity of many Cretaceous taxa, the majority of species in the present study have been left in open nomenclature or compared to existing species. The occurrence of *Bairdoppilata* species in the Trunch Borehole is summarized in Appendix 4.

Bairdoppilata cf. *B. pantaloensis.*

Pl. 3, fig. 10

cf.

Diagnosis. A large, trapezoidal species with a strongly arched dorsal margin and slightly drawn-out posterior; ventral margin convex.

Dimensions.	L	H
LV (MPK 11328)	0.95	0.56

Depository. MPK 11328

Material. 17 specimens

Remarks. The present material closely resembles the species to which it is compared, differing only in its smaller size and more convex ventral margin.

Range in this study. This species ranges in the outcrop samples from the Lower Campanian *Gonioteuthis quadrata* Zone (9), through the Upper Campanian into the Lower Maastrichtian Grey Beds of Trimingham (zone/subdivision 18). In the Trunch Borehole, it exhibits a more restricted range: Lower Campanian *G. quadrata* Zone (FAD SAG 514) to the middle of the Upper Campanian (LAD SAG 357). The range of this species in the Trunch Borehole is illustrated in Appendix 4, where it appears as species number 6.

Bairdoppilata septentrionalis (Bonnema, 1940)

Pl. 2, figs 20 -21; pl. 3, figs 3-6.

pars 1940 *Bairdia septentrionalis* Bonnema, pl. 2, figs 55-57, 60, 64, *non* pl. 2, figs 58, 59; pl. 3, figs 1-8.

non 1966 *Bairdoppilata septentrionalis* (Bonnema). Herrig, p. 771, fig. 45, pl. XII, figs 1, 2, 8.

1975a *Bairdoppilata septentrionalis* (Bonnema). Pokorny, pl. 1; pl. 2; pl. 3, figs 1-2; pl. 4, figs 1-3.

1975a *Bairdoppilata* ex. gr. *septentrionalis* (Bonnema). Pokorny, pl. 3, figs 3, 4; pl. 4, fig. 4.

1997 *Bairdoppilata septentrionalis* (Bonnema). Slipper, MS, pl. 6, figs 7, 8.

Diagnosis. See Pokorny, 1975a, p. 238 for a detailed diagnosis and description; also Slipper, MS.

Dimensions.	L	H
LV (MPK 11313)	0.91	0.55
RV (MPK 11316)	0.90	0.56
RV (MPK 113317)	0.88	0.50
RV (MPK 113318)	0.86	0.49

Depository. MPK 11313-11319

Material. An estimated 2000 specimens

Remarks. The present material is similar to Pokorny's illustrated specimens (from the Bonnema collection), but are particularly close to individuals assigned to *Bairdoppilata* ex. gr. *septentrionalis*. Pokorny (1975a, p. 246) recognizes that "as already noted, more than one species are lumped together as *B. septentrionalis.*" This species is very similar to *B. pseudoseptentrionalis* Mertens, 1956, originally described from the Upper Albian and Cenomanian of Germany and also recorded from France and England. A comparison of the two species shows a minor difference in that most LV specimens of the former species (from type locality) shows a straight antero-dorsal margin whereas the latter is gently convex. The similarity between the two species cannot, however, be ignored. Pokorny, writing on *B. pseudoseptentrionalis* (1975a) writes that "in view of its close similarity with *B. septentrionalis,* it is probable that both the species belong to the same lineage and may be discriminated as two chronological subspecies." This, however, is unproven. Slipper, MS, notes that "*B. pseudoseptentrionalis* Mertens, 1956 (*non. B. pseudoseptentrionalis* Mertens, 1956 *sensu* Weaver, 1982, pl. 4, figs 1-3) also has a distinct caudal process in both valves, but is distinguished by its convex posterodorsal margin. Weaver's specimens assigned to that species are more elongate, do not possess a distinct caudal process in the left valve, and have the posterior extremity well below mid-height. These should be considered as a distinct species."

Andreu, 1983, lists 11 species of *Bairdia* from the Upper Albian to Cenomanian of Spain, out of a total fauna of 215 species and subspecies, but does not illustrate or describe these. Andreu's material cannot, therefore, be compared or contrasted with the species seen in the present study.

Published range. Lower Santonian - Coniacian, Netherlands. Slipper, MS, notes its occurrence as a rare component through the Upper Turonian of Southern England.

Range in this study. This species ranges in the outcrop samples from the basal *coranguinum* Zone (Coniacian; zone 1) to the Lower Maastrichtian Grey Beds of Trimingham (zone 18). It is also abundant in the Trunch Borehole from its first appearance in the upper *Marsupites testudinarius* Zone of the Santonian (SAG 630). It is rather sporadic in the Lower Campanian, but is more abundant in the Upper Campanian, reaching its maximum abundance in the upper Beeston Chalk (SAG 312 - 14 specimens). In the Lower Maastrichtian, the species is present in both the pre-*Porosphaera* (SAG 231, 221, 217) and *Porosphaera* Beds (SAG 216, 213). The range of this species in the Trunch Borehole is illustrated in Appendix 4, where it appears as species number 1.

Bairdoppilata cf. *B. southerhamensis,* Weaver, 1982

Pl. 3, fig. 8

cf 1982 *Bairdoppilata southerhamensis* Weaver, p. 25, pl. 4, figs 4-6.

Diagnosis. A large species of *Bairdoppilata* with an elongate caudal process and high, strongly arched dorsal margin; anterior margin smoothly rounded; ventral margin strongly convex.

Dimensions.	L	H
LV (MPK 11326)	1.05	0.70

Depository. MPK 11326

Material. 7 specimens.

Remarks. Weaver's species is very similar in shape to the present material, but it is larger and there is a clear difference between LV and RV specimens. In the material of the present study only LV were seen and it is possible that some RV may have been attributed to a different species. *Bairdoppilata cretacea* (Van Veen, 1934) also has a caudal process, but is punctate.

Published range. The type level and locality of Weaver's species is the Middle Cenomanian of Southerham, Sussex. It is present from the uppermost Lower Cenomanian Chalk Marl (10) to mid-zone 13 (middle Upper Cenomanian Grey Chalk) in Southern England at various localities (Pitstone, Hertfordshire; Bluebell Hill, Kent; Barrington, Cambridgeshire; Glyndebourne, Sussex; Buckland Newton, Dorset; Culver Cliff, Isle of Wight). Johnson, 1996, also records the species from the Isle of Wight (Cenomanian to Turonian).

Range in this study. This species is restricted to the *coranguinum* Zone (Coniacian; zone/subdivision 3) in the outcrop samples of East Anglia. It was used in the biozonation as a marker for this substage (range biozone 1b). It was also present in the Santonian high *coranguinum* Zone in Essex in the Witham and Kelvedon Borehole (represented in this study by SAG 2057 and 2058).

Bairdoppilata sp. 1

Pl. 2, figs 13, 14

Diagnosis. A moderately thickly calcified species with a strongly arched dorsal margin and rounded anterior and posterior margins.

Dimensions	L	H
LV (MPK 11305)	0.91	0.56
LV (MPK 11306)	0.87	0.56

Depository. MPK 11305-11306.

Material. More than 300 specimens.

Remarks. *Bairdia cuvillieri* Damotte, 1971 subsp. *omnipraesens* Pokorny, 1975, from the Bohemian Lower Turonian to Coniacian is similar in shape but is significantly larger (0.91-1.35mm). Gründel's *Bairdia* sp. 1 (1966, pl. 1, fig. 6) is similar to several of the forms seen in the present study, but is generally larger (L=0.96mm) and appears punctate. Andreu, 1983, lists eleven species of *Bairdia* from the Upper Albian to Cenomanian of Spain, out of a total fauna of 215 species and subspecies, but does not illustrate or describe these. Andreu's material cannot, therefore, be compared or contrasted with the species seen in the present study. Although there are more than enough specimens to erect a new species, the present author did not feel justified in doing so, due to the difficulties in the taxonomy of this genus.

Range in this study. This species ranges from the basal *coranguinum* Zone of the Coniacian to the Lower Maastrichtian Grey Beds in the outcrop samples. It was also present in the Santonian high *coranguinum* Zone in Essex in the Witham and Kelvedon Borehole (SAG 2057 and 2058). In the Trunch Borehole, it first appears in the Lower Campanian (middle of the *O. pilula* Zone; FAD SAG 596) but is rather sporadic until the Upper Campanian, where it becomes more ubiquitous and occurs in numerous localities. It also appears in the Lower Maastrichtian pre-*Porosphaera* and *Porosphaera* Beds. The range of this species in the Trunch Borehole is illustrated in Appendix 4, where it appears as species number 2.

Bairdoppilata sp. 2

Pl. 2, fig. 15; pl. 3, figs 1, 2

Diagnosis. A large species with a strongly arched dorsal margin; trapezoidal and slightly elongate; moderately thickly calcified but rather variable in both size and shape.

Dimensions.	L	H
RV (MPK 11307)	0.89	0.50

Depository. MPK 11307, 11311, 1312

Material. 80 specimens.

Remarks. Andreu, 1983, lists eleven species of *Bairdia* from the Upper Albian to Cenomanian of Spain, out of a total fauna of 215 species and subspecies, but does not illustrate or describe these. Andreu's material cannot, therefore, be compared or contrasted with the species seen in the present study. Gründel's *Bairdia* sp. 1 (1966, p. 15, pl. 1, fig. 6) is similar to the present material, but is generally larger (L=0.96mm) and appears punctate. Bairdia sp. 2 (1966, pl. 1, figs 11-12) from the middle Upper Albian to Lower Cenomanian of Germany is also larger (0.96mm compared to 0.89mm). Although there are more than enough specimens to erect a new species, the present author did not feel justified in doing so, due to the difficulties in the taxonomy of this genus.

Range in this study. This species is long-ranging in the outcrop samples and extends from the Coniacian coranguinum Zone (3) to the Lower Maastrichtian Grey Beds (18).

In the Trunch Borehole, it ranges from the Lower Campanian *Gonioteuthis quadrata* Zone (9; FAD SAG 514) to the Lower Maastrichtian Porosphaera Beds (18). The range of this species in the Trunch Borehole is illustrated in Appendix 4, where it appears as species number 3.

Bairdoppilata sp. 3

Pl. 2, figs 16, 17

Diagnosis. A rather rounded valve with a strongly arched dorsal margin.

Dimensions.	L	H
LV (MPK 11308)	0.78	0.36

Material. 70 specimens.

Range in this study. In the outcrop samples, restricted to the Lower Campanian Gonioteuthis Zone (9) up into the 2 lowest samples of the Paramoudra Chalk at Crown Point Pit, Whitlingham.

The range of this species in the Trunch Borehole is illustrated in Appendix 4, where it appears as species number 5. It first appears in the lower part of the *Gonioteuthis quadrata* Zone (FAD SAG 540) and extends into the lowest sample of the Lower Maastrichtian (LAD SAG 231; pre-*Porosphaera* Beds).

Bairdoppilata sp. 4

Pl. 2, figs 12, 19.

Diagnosis. A large, inflated species with a strongly arched dorsal margin; a rounded anterior margin and a slightly drawn out, narrow posterior; appears heavily calcified.

Dimensions.	L	H
LV (MPK 11304)	1.03	0.57
LV (MPK 11313)	1.05	0.59

Depository. MPK 11304, 11313.

Material. More than 50 specimens.

Range in this study. This species is rare, ranging sporadically from the Lower Campanian (*Gonioteuthis quadrata* Zone - 9) into the Lower Maastrichtian *Porosphaera* Beds in the outcrop localities. In the Trunch Borehole, the species appears in appendix 4 as species 4; it first appears in the Lower Campanian (zone 9, FAD SAG 534 and ranges sporadically into the Lower Maastrichtian Porosphaera Beds (LAD SAG 216). It is rather more abundant in the Upper Campanian.

Genus NEONESIDEA Maddocks, 1969

Diagnosis. See Maddocks, 1969.

Taxonomic note. Recent members of the Bairdiinae were revised by Maddocks (1969) who erected 2 new genera *Neonesidea* and *Paranesidea* which, together with *Bairdoppilata* Coryell, Sample & Jennings, 1935, and *Triebelina* Bold, 1946 were used to accommodate many species previously referred to *Bairdia* McCoy, 1844, which was confined by Maddocks to the Upper Palaeozoic. In Titterton & Whatley's 1988 study of the abundant and diverse Recent bairdiids of the Solomon Islands, the authors note that "some difficulty was encountered in accommodating certain genera within established genera." Some species, for example, which seemed closest to *Neonesidea* had characteristics more diagnostic of *Paranesidea.* Pokorny (1980) erected a new subgenus: *Neonesidea (Maddocksia)* and describes 2 species from the Upper Cretaceous of Czechoslovakia. This reference is somewhat confused (pers. comm. Prof. Dr. E. K. Kempf, Dr Karel Wouters and Dr Ian Slipper - September 2001). The subgenus is characterised by the following characteristics: anteroventral and posteroventral margins of both valves bearing denticles; marginal denticles of *Neonesidea*

more numerous anteriorly and posteriorly. The range of *Maddocksia* is Upper Cretaceous to Recent but many authors do not consider it valid (pers. comm. Prof. R. C. Whatley, June 2000).

Remarks. Danielopol (1972) comments on the systematic position of the Bairdiidae, with observations on the morphology of antennae and limbs of several recent species of *Neonesidea* from the South Pacific.

?Neonesidea sp.

Pl. 3, fig. 13

Diagnosis. Trapezoidal in shape with strong antero-dorsal and postero-dorsal angles sloping to an extremely acute, pointed posterior and oblique anterior margin. Ventral margin broadly rounded for about half its length, rest of margin straight. Lateral surface smooth and featureless.

Dimensions.	L	H
RV (MPK 11323)	0.75	0.34

Depository. MPK 11323

Material. Fewer than five specimens.

Range in this study. Restricted to the Lower Campanian *Gonioteuthis* Zone.

Neonesidea sp. 1

Pl. 3, figs 7, 11-12, 14-15

Diagnosis. An elongate species with an arched dorsal margin; convex ventral margin with a slight concavity; narrow posterior and acute, upwardly turned caudal process; lateral surface smooth and does not appear to be thickly calcified.

Dimensions.	L	H
RV (MPK 11320)	0.75	0.36
RV (MPK 11322)	0.72	0.34

Depository. MPK 11320-11322, 11324-11325.

Material. Fewer than 10 specimens

Range in this study. This species ranges in the outcrop samples from the Upper Coniacian (*coranguinum* Zone - 3) to the Lower Maastrichtian pre-*Porosphaera* Beds, but it is absent throughout the Santonian and Lower Campanian, reappearing in the Upper Campanian basal *mucronata* Chalk (10)

Genus ALATANESIDEA Colin & Lauverjat, 1978.

Alatanesidea sp. Babinot, 1980

Pl. 3, fig. 16

1980 *Alatanesidea* sp, Babinot, p. 75, pl. 4, fig. 3

Diagnosis. A medium, elongate species with an arched dorsal margin; sinuous-convex ventral margin; narrow upturned caudal process; oblique anterior. Entire lateral surface finely punctate.

Dimensions.	L	H
RV (MPK 11327)	0.78	0.37

Material. Less than 5 specimens.

Remarks. The present material is almost identical to that figured by Babinot, 1980, but the lateral surface is smoother. It is also smaller and may possibly represent juvenile individuals.

Published range. The species was recorded from the terminal Cenomanian of Southern France.

Range in this study. Restricted in the outcrop samples to the Upper Campanian Paramoudra Chalk; absent in the Trunch Borehole.

Genus: CARDOBAIRDIA Van den Bold, 1960

Generic Diagnosis. Weaver, 1982, p. 26, "Shape ovate, valves usually heavily calcified; LV > RV, overlapping around entire margin, particularly dorsal and ventral. Hinge consists of crenulate terminal teeth separated by a weak median groove."

Remarks. Szczechura & Blaszyk, 1968, assign the genus to the suborder Metacopina, superfamily Healdiacea Harlton, 1933. They also give (pp. 186-188) a detailed history of the genus from its original designation by Van den Bold in 1960. The present author has, however, followed Weaver and most other authors and included the genus within the Bairdiidae.

Cardobairdia sp.

Pl. 3, figs 17-22

Diagnosis. A small, sub-ovate, slightly elongate species of *Cardobairdia*; arched dorsal margin and rounded anterior and posterior margins.

Dimensions.	L	H
LV (MPK 11329)	0.51	0.26
RV (MPK 11334)	0.46	0.24

Material. Fewer than 10 specimens

Depository. MPK 11329 –11334.

Remarks. Slipper (1997, pl. 6, figs 1-2) illustrates a new species from the British Turonian, *C. longitecta* which differs from the present material by its small posterior spine at the ventral margin of the RV. The present material is very similar to *C. minuta* (van Veen, 1936), as figured from the British Cenomanian by Weaver, 1982 (pl. 19, figs 15-19) and Wilkinson, 1988a (MS, pl. 23, figs 10-11). This species was originally placed in the genus *Krausella,* in its early synonomy (e.g. Van Veen, 1936; Bonnema, 1940; Oertli, 1958). It should be mentioned at this point, however, that Van den Bold did not originally include *K. minuta* in Cardobairdia but

noted the great similarity between it and species of this genus. Herrig (1966, p. 772, pl. 15, figs 1-4) used *Cardobairdia*, followed by later authors up to 1990. Wilkinson, 1988, in discussing the species, states that it "apparently has a very long range, having been recorded from the Aptian to Maastrichtian in northwestern Europe. However, it is very rare and more than one species is probably involved." The present material is, therefore, left in open nomenclature, following Nuyt's revision of *C. minuta* (1990). In this revision, three new species were erected from the Campanian of Belgium and the Cenomanian of Southern England. *Krausella minuta* (Triebel, 1940) was proved to be *nomen nudum* and, subsequently, many of the early records of *C. minuta* can be attributed to either *C. cenomanica* Nuyts, 1990 (p. 66, pl. 1, figs 1-4) or *C. triebeli* Nuyts, 1990. The former is illustrated by Witte *et al.*, 1992 (pl. 2, figs 5-7) but there is some discrepancy between the later work and those originally illustrated by Nuyts in 1990. However, the ostracods reported by Veen in 1936 belong to neither of these new species and the original *Krausella minuta* from the Maastrichtian of Holland remain unnamed (Witte *et al.*, 1992) and the syntypes have been lost. *Cardobairdia triebeli* has a more inflated shape and a more curved outline than *C. cenomaniensis* or the material of the present study. *C. rectimarginata* Nuyts, 1990 (Witte *et al.*, 1992, pl. 2, figs 8-9) is narrower and slightly more elongate.

Range in this study. This is a rare species with a sporadic occurrence; it is present in the Upper Campanian Upper Weybourne Chalk and Paramoudra Chalk. It also is a rare component in the Lower Maastrichtian *O. lunata* Chalk of Trimingham. In the Trunch Borehole, it is restricted to the Upper Campanian *B. mucronata* Zone Beeston Chalk (first appearing in sample SAG 345, LAD SAG 336).

Superfamily CYPRIDACEA Baird, 1845

Family PARACYPRIDIDAE Sars, 1923

Genus PARACYPRIS Sars, 1866

Treatise reference. Q 245

Treatise diagnosis. "Elongated, wedge-shaped, tapering to pointed posterior; LV > RV, very broad inner lamellae, bifurcating radial pore canals...."

Revised diagnosis (Maddocks, 1988, p. 55, based on both morphology of both hard and soft morphology; only the former characteristics are quoted here). "Carapace robust, smooth, elongate posteriorly, with arched to angulate dorsal margin, broadly rounded anterior margin, distinct ventral indentation, and narrowly rounded to acutely angulate posteroventral termination; greatest height and greatest thickness located anterior to midlength. Separate, deep anterior and posterior vestibules....zone of concrescence broad to very broad, with numerous regularly or irregularly branching radial pore canals and false radial pore canals; hinge lophodont, with a thin bar on the right valve; adductor muscle scar pattern paracyprid, consisting of three small regular scars in a curved anterior row and two posterior scars, plus a rectangular cap scar, which may be divided, located immediately above and only slightly larger than the three anterior scars, two mandibular scars, and one small frontal scar...."

Remarks. Maddocks (p. 53) makes the following statement about the genus: "For 120 years, *Paracypris* has been a conceptually monotypic genus, in spite of the hundreds of species that have been referred to it! The zoological concept of the genus has been based solely on the female of the type species, *Paracypris polita* Sars, 1866, for which no male has yet been described. Unfortunately, every one of the other genera in the subfamily Paracypridinae was also monotypic when proposed...Meanwhile, *Paracypris* early became a paleontogical dumping ground for hundreds of fossil species, most of which belong in other genera or families."

The 1988 paper extensively reviews the genus, listing living and recorded fossil species that should be retained within *Paracypris* and those which belong to other genera. The present author is sure that the forms assigned to the genus are true *Paracypris* since they conform closely to both the diagnosis given in the 1961 treatise and the emended diagnosis proposed by Maddocks, p. 55. The fact that the LV is larger than the RV is a diagnostic feature, whereby the genus can be distinguished from *Argilloecia* (RV > LV). Macrocypris differs in overlap, muscle scars and the presence of a clear hinge.

Paracypris sp. 1

Pl. 4, figs 1-3

Diagnosis. A medium species of *Paracypris,* elongate and without strongly concave ventral margin; rounded anterior and narrow, pointed posterior; dorsal margin weakly arched; posterior more pointed in RV than LV.

Dimensions	L	H
LV (MPK 11335)	0.60	0.26
RV (MPK 11336)	0.61	0.26

Material. At least 30 specimens

Depository. Catalogue numbers MPK 11335 – 11337 and various assemblage slides

Remarks. Similar to *Paracypris* sp. A of Cabral, 1998 (pl. 3, figs 11-13) from the Lower Aptian of Portugal but slightly less elongate.

Range in present study. This species is long ranging; Coniacian? to Lower Maastrichtian. It is present in the Coniacian, however, only in the basal *coranguinum* zone and is not seen at all in the Santonian. It appears again in the Lower Campanian restricted *quadrata* zone (9) and is present in the Upper Campanian basal *mucronata* and lower levels of the Eaton Chalk, as well as in the Beeston and Paramoudra chalks (zones/subdivisions 10, 11,13 and 14). It also occurs in the Lower Maastrichtian pre-*Porosphaera* Beds of Sidestrand (15) and the *O. lunata* Chalk of Trimingham (17). In the Trunch Borehole, it ranges from the Upper Campanian (basal *mucronata* Chalk) to Lower Maastrichtian.

Paracypris sp. 2

Pl. 4, fig. 4

Diagnosis. A small, narrow and elongate species, posterior margin drawn out and pointed; anterior margin rounded.

Dimensions.	L	H
LV (MPK 11338)	0.55	0.23

Material. At least 15 specimens

Remarks. Differs from sp. 1 of this study, by its shape and size (narrower, smaller, more elongate). More elongate than *Paracypris jonesi* Bonnema, 1940, from the Schreibkreide of the Netherlands.
Range in this study. Not seen in the Trunch Borehole; appears restricted to the basal *mucronata* Chalk of Eaton and Cringleford, also seen in the Upper Campanian assemblages at Catton Grove and Keswick.

Paracypris sp. cf. *P. wrothamensis* Kaye, 1965

Pl. 4, figs 5-9.

cf. 1965 a. *Paracypris wrothamensis* Kaye, pl. 9, figs 9-14
1982. *Paracypris* aff. *P. wrothamensis* Kaye. Weaver, pl. 4, figs 13 –14.
1988. *Paracypris wrothamensis* Kaye. Wilkinson, p. 161, pl. 3, fig. 22.
1992. *Paracypris wrothamensis* Kaye. Witte *et al.*, pl. 2, fig. 10.

Diagnosis. A large species of *Paracypris*; valves very elongate, thin shelled and fragile, frequently broken. Dorsal margin strongly arched, anterior margin broadly rounded, posterior drawn out to a sharp point.

Dimensions.	L	H
LV (MPK 11339)	0.90	0.35

Depository. Catalogue numbers MPK 11339 – 11343 and several assemblage slides.
Material. At least 15 specimens
Remarks. The present material is rather similar to Weaver's specimens from the British Cenomanian, showing a similar size difference (smaller than Kaye's nominative species from the Albian of Southern England). The specimens are also similar to those illustrated by Wilkinson in 1988 and Witte *et al.*, 1992.
Range in present study. This species is restricted to the Upper Campanian and Lower Maastrichtian in the outcrop localities and is present in the basal *mucronata* Chalk of Eaton and Cringleford (Zone/subdivision 10), from the Paramoudra Chalk of Crown Point Pit, Whitlingham (14) and from the Lower Maastrichtian *O. lunata* Chalk and Grey Beds of Trimingham (17 and 18 respectively).

Family.CYPRIDIDAE Baird, 1845
Subfamily. CYPRIDINAE Baird, 1845
Genus ARGILLOECIA Sars, 1866

Treatise reference: Q 247
Treatise diagnosis: " Sub-elliptical, nearly cylindrical in cross section; mid-portion of shell somewhat flattened; RV >LV. Inner lamella typically very broad. Marked sexual dimorphism, males being much smaller and more elongate than females."

Argilloecia argillos sp. nov.

Pl. 4, figs 10-18

Derivatio nominis: Gr. αργιλλοζ argillos: white clay, with reference to the occurrence of this species in the white Upper Chalk.
Holotype. Carapace, MPK 11345
Type locality. Upper Campanian, basal *mucronata* Chalk, Cringleford, Norfolk, SAG 107.

Diagnosis. A medium species of *Argilloecia*, distinguishable from most other Cretaceous representatives of the genus by its elongate valves, arched dorsal margin and acutely pointed posterior.

Description. Medium to large. Elongate subovate to sublunate. Valves of different shape. Anterior margin well-rounded in RV, more angular in LV with very marked angle antero-dorsally; apex at mid-height in RV, above mid-height in LV. Posteriorly margin acutely pointed in LV, less so in RV., apex sub-ventral in both valves. Dorsal margin regularly arched with apex at mid-length. Ventral margin with pronounced median concavity. RV considerably larger than LV, with strong dorsal; overlap. Smooth. Internal features as for genus. Sexual dimorphism not observed.

Dimensions.

	L	H
Holotype, C (MPK 11345)	0.69	0.27
Paratype, C (MPK 11344)	0.66	0.27
Paratype, RV (MPK 11346)	0.72	0.28
Paratype, RV (MPK 11347)	0.66	0.27
Paratype, LV (MPK 11348)	0.62	0.25
Paratype, LV (MPK 11349)	0.62	0.25
Paratype, LV (MPK 11350)	0.61	0.26
Paratype, LV (MPK 11351)	0.61	0.26

Material. At least 500 specimens.

Remarks. This species differs from *Argilloecia cretula* sp. nov. in size (slightly smaller) and shape (more elongate, narrower; posterior margin acute and pointed, ventral margin concave; dorsal margin strongly arched). The latter species is larger, broader, with rounded anterior and dorsal margins, a less arched dorsal margin and an almost straight ventral margin and its two valves are similar in shape. *Argilloecia gracilis* Bonnema, 1940, (Pl. 2, figs 24-26) from the Upper Cretaceous Schreibkreide of the Netherlands is a smaller species, similar in shape but less elongate, posterior margins less acute, dorsal margin less arched. *A. constricta* Holden, 1965 (p. 403, text fig. 9a-c), from the Rosario (Upper Cretaceous) Formation of California is similar in size but differs in its less elongate, truncated posterior The material of the present study lacks the "small anterodorsal flange and conspicuously laterally flattened carapace" of Holden's species.

Alexander (1935) described *Argilloecia taylorensis* (p. 356, text fig. 1a, 1b) from the Upper Taylor (Upper Campanian) Formation of Onion Creek, Texas. This species differs from *A. argillos* sp. nov. in its smaller size and is broader and less elongate with a more evenly rounded anterior margin and obtuse posterior and nearly straight ventral margin.

Range in this study. In both the outcrop samples and those of the Trunch Borehole, this species exhibits a shorter range than *A. cretula*. In the outcrop samples, it first appears in the restricted *quadrata* Zone (9) and is present throughout the Upper Campanian (basal mucronata Chalk to Paramoudra Chalk; zone/ subdivisions 10-14). The species is ubiquitous in the pre-Weybourne -4 and basal *mucronata* Chalk at Cringleford and the Middle Weybourne Chalk at Keswick. It is present throughout the basal mucronata mucronata Chalk, Eaton and Upper Weybourne Chalk at Eaton, Norfolk and was recorded at Stoke Holy Cross and in the assemblages at Catton Grove. *A. argillos* is ubiquitous in the Beeston Chalk at Caistor St Edmunds and West Runton, Norfolk and in the Paramoudra Chalk at Whitlingham. The species crosses the Campanian-Maastrichtian boundary and occurs in all samples from the pre-*Porosphaera*

Beds of Sidestrand (15) and *O. lunata* Chalk of Trimingham (17), and all but one sample from the Grey Beds of Trimingham (18). In the Trunch Borehole, it does not appear until later in the *G. quadrata* Zone (First Appearance Datum - SAG 488). It is present throughout the Upper Campanian (10-14), but does not extend into the Lower Maastrichtian.

Argilloecia cretula sp. nov.

Pl. 4, figs 19-26

Derivatio nominis: L. creta, cretula, chalk, white earth or clay, with reference to the occurrence of this species in the Upper Chalk of East Anglia.

Holotype. RV (MPK 11355)

Type locality and level. Upper Campanian, Eaton Chalk, Eaton, Norfolk, SAG 94.

Diagnosis. A medium species of *Argilloecia*, characterized by its broad valves, rounded anterior and posterior, dorsal margin only weakly arched; ventral margin nearly straight.

Description. Medium. Elongate subovate. Valves of similar shape. Anterior margin rather narrowly rounded about a blunt apex at mid-height. Posterior margin with long convex postero-dorsal slope and subventral pointed apex (sharpest in female). Dorsal margin gently convex but straight medianly in male. Ventral margin with very subdued median concavity. Greatest length below mid-height; greatest height at about mid-length. Smooth. Internal features as for genus.

Dimensions.	L	H
Holotype, RV (MPK 11355)	0.69	0.27
Paratype, RV (MPK 11353)	0.72	0.27
Paratype, RV (MPK 11354)	0.72	0.27
Paratype, RV (MPK 11356)	0.73	0.27
Paratype, RV (MPK 11357)	0.73	0.27
Paratype, RV (MPK 11358)	0.73	0.27
Paratype, LV (MPK 11359)	0.68	0.26
Paratype, LV (MPK 11360)	0.68	0.26

Material. More than 1000 specimens.

Remarks. This species differs from *Argilloecia argillos* sp. nov and *A. gracilis* Bonnema, 1940, in terms of its size (slightly larger), shape (less elongate, broader, posterior margin rounded, ventral margin nearly straight, dorsal margin less strongly arched). The latter species is smaller, narrower and more elongate, with rounded anterior and a pointed posterior; dorsal margins strongly arched, ventral margin concave. The present material is very similar to *Argilloecia communis* Bonnema, 1940 (pl. 2, figs 18-20) in shape, but is larger, with a less arched dorsal margin; it is also less elongate. *A. taylorensis* Alexander (1935, p. 356, text figure 1a, 1b) from the Upper Taylor Formation (Upper Campanian) of Onion Creek, Texas, differs from *Argilloecia cretula* sp. nov. in its smaller size. It is broader and less elongate, with a more evenly rounded anterior margin and obtuse, less rounded posterior.

A third form, which appears in some of the stratigraphical distribution charts as *Argilloecia* sp., is very similar in shape to *cretula* and may, on further, more detailed study, be attributed to this species.

Range in this study. The species ranges in the outcrop samples from the Coniacian to Lower Maastrichtian. It first appears in the middle of the basal *coranguinum* Zone (1) but is absent in much of

the low *coranguinum* Zone (2), occurring only in the top sample (SAG 19) at Euston, Suffolk. It is more common in the uppermost zone of the Coniacian (3 - *coranguinum* Zone), where it is present at both Litcham and South Pickenham, Norfolk. At the latter locality, it is particularly abundant in SAG 114 (7.6% of the assemblage) and SAG 115 (7%). *A. cretula* occurs in the Santonian, only in the upper samples of the high *coranguinum* Zone (4), but the species is better represented in the *Uintacrinus socialis* and *Marsupites testudinarius* zones (5 and 6) at Stanton, Suffolk and Houghton St Giles, Norfolk, respectively. It was also seen in both the Kelvedon and Witham boreholes (upper *M. testudinarius* Zone, Essex). In the Lower Campanian, the species occurs in the *O. pilula* Zone (7), *pilula*/restricted *quadrata* Zone (8) and the restricted *quadrata* Zone (9) at various localities. It is, however, more abundant in 9 and is present throughout the Upper Campanian (Zone/subdivisions 10-14; basal *mucronata* Chalk, Eaton, Weybourne, Beeston and Paramoudra chalks) at various localities around Norfolk. It ranges across the Campanian - Maastrichtian boundary and occurs in the pre-*Porosphaera* and *Porosphaera* beds of Sidestrand (15, 16) and the *O. lunata* Chalk and Grey Beds of Trimingham (17, 18). In the Trunch Borehole, the species first appears in the top sample of the Santonian *M. testudinarius* Zone (FAD SAG 630), and occurs subsequently in the upper part of the Lower Campanian Zone 7 and the upper part of Zone 9. It is present in all divisions of the Upper Campanian and is also present in the pre-*Porosphaera* and *Porosphaera* Beds of the Lower Maastrichtian (15, 16).

Family PONTOCYPRIDIDAE Müller, 1894

Genus PONTOCYPRELLA Ljubimova, 1955

Diagnosis: as of Weaver, 1982, p. 29; "elongate, reniform with arched dorsal margin and straight to weakly concave ventral margin. LV > RV."

Remarks. This genus was originally placed in the Pontocypridinae but was moved into the Paracyprididae by Swain (*Treatise*, 1961). Weaver (1982) regards it as belonging in the Pontocypridinae, "on the basis of its smooth surface, arched dorsal margin, rounded anterior and more pointed posterior ends, and muscle scars consisting principally of 3 elongate sub-divided scars."

Pontocyprella sp.

(not illustrated)

Diagnosis. A medium species of *Pontocyprella* with a weakly convex dorsal margin and a nearly straight ventral margin; equally rounded posterior and anterior margin in LV, in RV, posterior margin more narrowly rounded.

Dimensions.	L	H
LV (Coniacian, from SAG 113),	0.66	0.32
RV (Coniacian, from SAG 113)	0.61	0.28

Material. at least 25 specimens.

Remarks. This species is rather like Weaver's *Pontocyprella hindei* (1982, p. 30, pl. 4, figs 15-16), later illustrated by Witte *et al.*, 1992 (pl. 2, fig. 13) but is slightly larger; differs from *P. robusta* in its smaller size, less heavily calcified valves, less strongly arched dorsal margin and straight ventral margin. The

present material differs from *P. harrisiana* (Jones, 1849), illustrated by Weaver, 1982 (pl. 4, figs 17-20) by its narrower valves and more pointed posterior, the ventral margin, especially in the RV is less concave.

Range in this study. This species shows a more sporadic range than *P.* sp. cf. *P. robusta.* It first appears in the.Coniacian *coranguinum* Zone at South Pickenham and Litcham, but is not seen in the Santonian. It reappears again in a single sample of the Lower Campanian restricted *quadrata* Zone and is a sporadic component of the Upper Campanian basal *mucronata* Chalk at Eaton, but is not seen in the higher levels at that locality. It also occurs in the basal *mucronata* Chalk at Cringleford.

It was not seen in the Beeston Chalk, but has been recorded at Keswick (Weybourne Chalk, Weybourne [2] according to the zonal scheme of Wood, 1988). It was present also in the Paramoudra Chalk of Crown Point Pit, Whitlingham, and in a single sample from Catton Grove (Weybourne [3] according to Wood), but does not occur above the Upper Campanian Paramoudra Chalk. In the Trunch Borehole, it ranges from the *O. pilula* Zone of the Lower Campanian to the Upper Campanian Paramoudra Chalk.

Pontocyprella sp. cf. *P. robusta* Weaver, 1982

Pl. 4, figs 27–30.

cf 1982 *Pontocyprella robusta* Weaver, p. 30, pl. 4, figs 21, 22; pl. 5, figs 1, 2

Diagnosis. A sub-cylindrical, elongate-ovate species of *Pontocyprella* with an asymmetrically rounded anterior margin and a more narrowly rounded posterior margin; both margins with apex below mid-height.

Dimensions.	L	H
RV (MPK 11362)	0.68	0.34
LV (MPK 11363)	0.66	0.33

Depository. MPK catalogue numbers 11361–11364 and various assemblage slides.

Material. At least fifty specimens.

Remarks Weaver (1982, p. 31) first reported the species from the Upper Cenomanian of Kent. The material of the present study is very similar, but slightly smaller and less heavily calcified than the Cenomanian material. Johnson (1996) records it from the plenus Marls, Isle of Wight.

Colin, 1973, illustrates *Pontocyprella* sp. 1 (pl. 1, fig. 6) from the Upper Campanian of Southwestern France. This species is similar to the present material but is larger and slightly more inflated. *Pontocyprella inflexa* (Gründel, 1974, pl. 1, fig. 14) from the Santonian of Salzburg differs in its stronger and more convex dorsal margin. Oertli, 1958, illustrates *P. maynci* from the Aptian-Albian of France this species is more inflated than *P. robusta* and the present material, with convex dorsal and ventral margins, rounded anterior and posterior margins. The specimens from the Albian (pl. 2, figs 46-54) appear more like *Cytherella,* the Aptian specimens are more like *Pontocyprella* (pl. 3, fig. 55-60).

Range in this study. Coniacian to Lower Maastrichtian. The species first appears in the Coniacian *coranguinum* Zone at South Pickenham and Litcham, extending across the Santonian high *coranguinum, Uintacrinus* and *Marsupites* Zones. It is present in the Lower Campanian *pilula* and restricted *quadrata* Zones and also in the Upper Campanian basal *mucronata* Chalk at Eaton, but absent in the higher horizons at this locality. It was also seen in the basal *mucronata* Chalk at Cringleford and is a relatively constant component of the assemblages at Catton Grove and Keswick. It also occurs in the Beeston

Chalk at Caistor St Edmunds, but is restricted to a single sample (SAG 55). It is present in the Paramoudra Chalk at Whitlingham and Asylum Pit, Thorpe. The species is less abundant in the Lower Maastrichtian; at Trimingham, it was found in the *O. lunata* Chalk but not in the overlying Grey Beds, at Sidestrand (stratigraphically higher than Trimingham), it was restricted to a single sample at the top of the Pre-*Porosphaera* Beds.

Superfamily CYTHERACEA Baird, 1850.

Family BYTHOCYTHERIDAE Sars, 1926.

Genus BYTHOCERATINA Hornibrook, 1952.

Treatise reference Q 268

Treatise diagnosis. "Like *Monoceratina* but hinge differs in having long denticulate median element to otherwise lophodont hinge. Some species with caudal process below hinge line as in *Bythocythere*, but others have this process in line with the hinge (as *Monoceratina*). Range: Cretaceous to Recent.

Weaver's extended diagnosis (1982, p. 37): " Outline usually sub-rectangular to triangular; posterior usually produced into a caudal process which terminates above mid-height. Surface usually reticulate, but may be pitted, smooth or with lateral nodes; lateral spine with fairly narrow base. Hinge of left valve consisting of smooth terminal sockets separated by a smooth to crenulate median bar. Terminal sockets may not be developed in some species."

Remarks. This genus, although originally erected for species similar in shape to *Monoceratina*, differs in the shape of its type species (*B. mestayerae* Hornibrook, 1952, and *M. ventrale*, Roth, 1928 respectively). *Bythoceratina* generally differs from *Monoceratina* in its stronger ornament, less strongly inflated valves and more prominent lateral spine. *Cuneoceratina* Gründel and Kozur, 1971, was regarded by Weaver as a sub-genus of *Bythoceratina*. However, the present author has accorded it full generic status. The former may be distinguished by its sub-triangular outline with a more drawn out posterior and a longer, narrower lateral spine. Weaver notes that Gründel and Kozur's genus comprises "a small group of closely related species from the Upper Cretaceous".

Bythoceratina bonnemai (Kaye, 1964)

Pl. 5, figs 1-3.

1964 *Monoceratina bonnemai* Kaye, p. 52, pl. 3, figs 5-6

1982 *Bythoceratina (Bythoceratina) bonnemai* (Kaye). Weaver, pl. 6, figs 5-6.

1988a *Bythoceratina (Bythoceratina) bonnemai* (Kaye). Wilkinson, MS, pl. 4, fig. 11.

1988b *Bythoceratina (Bythoceratina) bonnemai* (Kaye). Wilkinson, pl. 1, fig. 5.

Diagnosis. Valves smooth, elongate; dorsal and ventral margins straight and parallel. Posterior margin broken; median sulcus present. Postero-ventral spine evident, a second one possible but obscured due to damage to specimens. Large, bulbous, spherical node on antero-dorsal surface; faint ridge along postero-dorsal margin. Hinge very poorly preserved; a smooth groove in RV, smooth bar in LV.

Dimensions.	L	H
Damaged RV (MPK 11364)	0.70	0.29
LV (MPK 11365)	0.73	0.31

Material. Three specimens only.

Remarks. Kaye notes that "the ornament of this species is quite unlike any other published Cretaceous species." The specimens of the present study are closer to Weaver's Cenomanian specimens but show a small postero-dorsal spine not seen in the earlier records. This, however, is assumed to be simply a morphological variation resulting from further development of this species over time. The specimens of the present study are slightly smaller than those of Kaye, but slightly larger than Wilkinson's quoted measurements. In Wilkinson's illustrated specimens (for example pl. 4, fig. 11, LV). the bulbous spherical node is slightly less prominent. Wilkinson considers *B. bonnemai* to be a geographically restricted species known only from Kaye and Weaver's records from Southern England, but also records it from East Anglia. It is entirely possible that the specimens from the Late Campanian of Norfolk belong to an entirely different, closely related species than those from the Cenomanian but there is not sufficient material to prove or disprove this link in phylogeny. The present author considers that, until such a question is answered, it is logical to retain these specimens within *B. bonnemai.*

Initially, Kaye placed the species in *Monoceratina* but, since there are two lateral spines and not one, it is now correctly assigned to *Bythoceratina.* Both Weaver and Wilkinson use *Bythoceratina (Bythoceratina)* but, for simplicity, this study refers to the species as *Bythoceratina,* without the need for the additional use of a subgenus.

Published range Kaye first reported the species from the Cambridge Greensand of Barrington, Cambridgeshire. Weaver (1982) found it in the Glauconitic Marl Beds of Southern England and Wilkinson (1988a, MS; 1988b) reports it from the early Cenomanian Chalk Marl of the Grantchester Cutting

Range in this study. Restricted to the upper horizons of the Upper Campanian and the Lower Maastrichtian. It is present as a rare component in the Paramoudra Chalk at Crown Point Pit, Whitlingham, and is also present in the Pre-*Porosphaera* Beds of Sidestrand.

Bythoceratina umbonata umbonata (Williamson, 1847)

Pl. 5, figs 15-20.

1847 *Cytherina umbonata* Williamson, p. 82, pl. 4, fig. 78

1849. *Cythere umbonata* (Williamson). Jones, p. 12, pl. 2, fig. 3a-d

non. fig. e [= *B. (B.) umbonata magna* Weaver, 1982.

1870 *Cytheropteron umbonatum* (Williamson). Jones, p. 74, 76.

1890. *Cytheropteron umbonatum* (Williamson). Jones & Hinde, p. 40, pl. 1, figs 21-24, 26,

non fig. 25 [= *B. (B.) umbonata magna* Weaver, 1982].

1893. *Cytheropteron umbonatum* (Williamson). Chapman & Sherborne, p. 347.

non. 1934 *Monoceratina umbonata* (Williamson). Alexander, p. 62, pl. 8, fig. 9,

1941. *Monoceratina umbonata* (Williamson). Bonnema, p. 29, pl. 6, figs 54-62.

1964. *Monoceratina umbonata* (Williamson). Kaye, p. 56, pl. 3, figs. 3, 4, 7.

1964. *Monoceratina umbonata* (Williamson). Gründel, p. 48, pl. 8, figs 29-31.

1971. *Bythoceratina* sp. 733, aff. *umbonata* (Williamson). Damotte, pl. 6, fig. 12.

1978. *Bythoceratina (Bythoceratina) umbonata* (Williamson) Neale, pl. 13, fig. 13, *non.* fig. 14.

1982. *Bythoceratina (Bythoceratina) umbonata* (Williamson). Weaver, p. 39, pl. 6, figs 10-13.

1988a. *Bythoceratina umbonata umbonata* (Williamson). Wilkinson, MS, pl. 1, fig. 3.

1988b. *Bythoceratina umbonata umbonata* (Williamson). Wilkinson, pl. 4, fig. 12.

1992 *Bythoceratina umbonata umbonata* (Williamson). Witte *et al.*, pl. 3, fig. 10.

1992. *Bythoceratina umbonata* (Williamson) *glabra*. Weaver, 1982. Witte *et al.*, pl. 3, fig. 12.

Diagnosis. A medium, rather inflated species with parallel dorsal and ventral margins, a stout lateral spine and broad medium sulcus; strongly ornamented, ornament covering entire lateral surface.

Dimensions.	L	H
LV (MPK 11379)	0.75	0.41
LV (MPK 11380)	0.73	0.43
LV (MPK 11381)	0.75	0.43
RV(MPK 11382)	0.76	0.45

Material At least 130 specimens

Remarks. The specimen assigned by Damotte (1971) is assigned to *B.* aff. *umbonata* but is very similar to the present material and previously illustrated specimens. It is, therefore, included in synonomy with the nominative species. *M. umbonata* as illustrated by Alexander (1934, p. 62) is not considered to be conspecific with Williamson's species. It differs in its extremely straight anterior margin and dense surface ornamentation.

Weaver (1982) erected a new subspecies, *B. umbonata glabra*, from the Lower Cenomanian of Southeast England (pl. 6, fig. 17-19). This is generally more inflated and strongly calcified than the nominative species. Weaver erects an additional subspecies, *B. umbonata magna* (1982, pl. 6, fig. 14-16; Ellis and Messina Catalogue of Ostracoda, Book 56, supplement 36, for 1990), which is larger than *B. umbonata umbonata* and also lacks a hinge ear. Witte *et al.*, 1992, illustrate Weaver's subsp. *glabra* from the Cenomanian of the eastern Netherlands. This, however, appears to be closer to the nominative subspecies than to Weaver's figured material. *B. umbonata* (in the range charts in chapter 3, this is used to indicate the nominative subspecies) and the present author has included Witte's material in synonomy with this subspecies. This species differs from *B. umbonatoides* (Kaye) in its sharper caudal termination. It is also flatter antero-laterally, lacking the swelling in front of the median sulcus.

In the present study, this record is the highest for the species in Britain; all previous records restrict it to the Cenomanian, earliest Turonian.

Published range. This appears to be a long ranging species. King (1968) regards it as being "most typical of the Albian and Cenomanian, being rarer in the higher Chalk, where it tended to be replaced by *B. umbonatoides*."

Lower Cenomanian – Switzerland (Damotte *et al.*, 1981); Lower to Upper Cenomanian – eastern Netherlands (Witte *et al.*, 1992), Isle of Wight (Hart *et al.*, 1987).

Cenomanian to Upper Turonian – Spain (Babinot *et al.*, 1992).

Cenomanian to Albian – Cambridge Greensand, Wilkinson, 1988a, MS.

Albian – France and England (Damotte *et al.*, 1981).

Albian to Coniacian of Germany (Gründel, 1964).

Range in this study. In the outcrop localities, this species first appears in the basal *coranguinum* Zone of the Coniacian. It disappears in the Santonian high *coranguinum* Zone and reappears in the *Uintacrinus* Zone, but is absent in the succeeding *Marsupites* Zone and Lower Campanian. It is more common in the

Upper Campanian basal *mucronata* Zone, occurring at Cringleford and Eaton, and is almost ubiquitous in the Paramoudra Chalk assemblages of Crown Point Pit, Whitlingham, and at Asylum Pit, Thorpe, near Norwich. The species is also seen in the *O. lunata* Chalk and Grey Beds of Trimingham and the Pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand.

In the Trunch Borehole, this species has a slightly shorter range; it first appears in the Lower Campanian *G. quadrata* Zone and disappears just below the Campanian–Maastrichtian boundary (LAD = SAG 277) in the Upper Campanian Paramoudra Chalk. It is absent in the Lower Maastrichtian.

Bythoceratina umbonatoides umbonatoides (Kaye, 1964a)

Pl. 5, figs 4-14.

1964 *Monoceratina umbonatoides* Kaye, p. 57, pl. 4, figs 2, 5.
1965 *Bythoceratina umbonatoides* (Kaye). Damotte, pl. 6, figs 5-8
1967 *Bythoceratina umbonatoides* (Kaye). Herrig, p. 607, text figs 1-6.
1971a *Bythoceratina umbonatoides* (Kaye). Damotte, p. 98, pl. 6, fig. 10a-c.
1978 *Bythoceratina umbonatoides* (Kaye). Neale, pl. 14, figs 2-6.
1982. *Bythoceratina umbonatoides umbonatoides* (Kaye). Weaver, pl. 6, figs 6-9
1988a *Bythoceratina umbonatoides umbonatoides* (Kaye). Wilkinson, MS, pl. 4, fig. 15.
1988b. *Bythoceratina umbonatoides umbonatoides* (Kaye). Wilkinson, pl. 1, fig. 2.

Diagnosis. A medium species of *Bythoceratina* characterised by its inflated anterolateral area; reticulate surface; smooth area posterior to broad medium sulcus. Valves sub-rectangular and strongly calcified; dorsal and ventral margins straight to weakly concave and parallel; anterior margin symmetrically rounded in LV (obliquely rounded in RV).

Dimensions	L	H
RV male (MPK 11374)	0.69	0.39
LV female (MPK 11369)	0.64	0.41

Depository. MPK catalogue numbers 11367 to 11378.

Material. Over 100 specimens.

Remarks. This species differs from *B. umbonata* in the strong inflation of the antero-lateral area. A large node is usually situated antero-dorsally of the median sulcus. Kaye (1964) notes that, in Britain, the species is restricted to the Upper Chalk and is "probably a direct descendant of *B. umbonata.*" Weaver (1982) and Wilkinson (1988) have extended the range back to the Cenomanian but the species is still most abundant in the Upper Chalk. Herrig, 1966, in describing the species, divides it into "form groups" and adds a new subspecies *Bythoceratina umbonatoides insolata. Bythoceratina umbonatoides umbonatoides* appears to be a morphologically variable species, with variations in size, shape and degree of ornament. This degree of variation was also seen in the material of the present study but subdivision into form groups according to Herrig's definition was not considered necessary.

The present material conforms closely to the specimens illustrated by previous authors. Those illustrated by Damotte (1965, 1971a) from the Campanian of the Paris Basin and by Neale (1978) from the Upper Chalk, *coranguinum* Zone of Sonning, Berkshire, are identical and all show the diagnostic characteristics

for the species particularly clearly. The present author has examined several slides of Kaye's Upper Cretaceous material containing this species, and a slide of ostracods picked from the Sonning locality (seen by the present author in the UW Aberystwyth Micropalaeontology collections, prior to their move to the Natural History Museum, London). *Bythoceratina umbonatoides umbonatoides* from this source was found to be identical with that of the present study and showed a similar diversity in size and ornament. Weaver, 1982, describes *Bythoceratina umbonata magna* from the Lower to Middle Cenomanian of Southeast England. Some similarities exist with *Bythoceratina umbonatoides umbonatoides* but the former lacks a distinct inflated area and the smooth area posterior to the median sulcus.

Range in the present study. Upper Coniacian to Lower Maastrichtian. In the outcrop samples, the species first appears in the upper levels of the *coranguinum* Zone, and is particularly abundant in SAG 115, South Pickenham. It is absent in the Santonian, reappearing in the uppermost Lower Campanian restricted *quadrata* Zone, but is rare until the Upper Campanian. It is almost ubiquitous in the assemblages at Eaton, appearing as a constant and relatively abundant component in the basal *mucronata* Chalk and through the Eaton Chalk and Upper Weybourne Chalk. It is absent at Stoke Holy Cross, where the diversity of species of *Bythoceratina* is also low. It occurs in the Beeston Chalk at Caistor St Edmund and is present in the Paramoudra Chalk of Crown Point and Asylum Pits, but not as abundantly as in lower horizons. The species extends up into the Lower Maastrichtian, an extension of the stratigraphical range since it was previously considered to extend from the Upper Coniacian to the Campanian-Maastrichtian boundary. In the present study, It was recorded in the *O. lunata* Chalk and Grey Beds of Trimingham, and in the stratigraphically higher Pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand. In the Trunch Borehole, it first appears in the *G. quadrata* Zone (9) of the Lower Campanian, extending up into the Paramoudra Chalk (LAD SAG 267).

Bythoceratina sp. 1

Pl. 5, figs 21, 22.

Diagnosis. A rather elongate and finely reticulate species of *Bythoceratina*, Dorsal and ventral margins straight and parallel; anterior margin rounded.

Dimensions.	L	H
RV (MPK 11385)	0.59	0.27
RV (MPK 11386)	0.57	0.28

Material. 12 specimens

Remarks. This species is similar to *Bythoceratina umbonatoides umbonatoides* (Kaye) but is distinguished by its smaller size, slightly more elongate shape and finer reticulate ornament.

Range in present study. Upper Coniacian to Lower Maastrichtian.

This species has a relatively long range in the outcrop samples. It first appears in the upper *coranguinum* Zone of the Coniacian, but is absent in the Santonian and very rare (restricted to a single sample) in the Lower Campanian restricted *quadrata* Zone. It is more common in the Upper Campanian and is present in the basal *mucronata* Zone at Eaton, extending up into the Eaton and Upper Weybourne Chalks at this locality. It is present also at Stoke Holy Cross, in all the samples at Keswick, and in the basal *mucronata* Chalk and basal Eaton Chalk at Cringleford. The species also occurs in the Beeston Chalk at Caistor St Edmund and is a regular component of assemblages in the Paramoudra Chalk of Crown Point Pit,

Whitlingham. It is less common in the Lower Maastrichtian, occurring as a rare and rather sporadic component in the Grey Beds of Trimingham and the Pre-*Porosphaera* Beds of Sidestrand. In the Trunch Borehole, it is present in Zones 9 (*G. quadrata*, Lower Campanian) and 16 (Porosphaera Beds, Lower Maastrichtian).

Bythoceratina sp. 2

Pl. 5, fig. 23

Diagnosis. An elongate species with a straight dorsal margin, rounded anterior and posterior margins and a slightly concave ventral margin; shallow median sulcus; ornament weak and covers only middle of lateral surface. Margins smooth; postero-ventral spine strong.

Dimensions.	L	H
LV (MPK 11387)	0.61	0.29

Depository. MPK 11387.

Material. Less than 10 specimens.

Range in the present study. This species ranges from Coniacian to Lower Maastrichtian in the outcrop samples but was restricted in the Trunch Borehole to the Lower Campanian (*G. quadrata* Zone) and the Lower Maastrichtian *Porosphaera* Beds.

In the outcrop samples, it first appears in the Coniacian *coranguinum* Zone but is absent in the Santonian and Lower Campanian. It is present in the upper levels of the basal *mucronata* Chalk at Cringleford and sporadically in the basal *mucronata*, Eaton and Upper Weybourne Chalk at Eaton. It was also recorded from two samples of the Paramoudra Chalk at Whitlingham. In the Lower Maastrichtian, it was seen in the Grey Beds of Trimingham and the Pre-*Porosphaera* Beds of Sidestrand. In the Trunch Borehole, the range is sporadic and the species occurs in the Lower Campanian G. quadrata Zone (9) and Lower Maastrichtian Porosphaera Beds (16)

Bythoceratina sp. 3

Pl. 5, fig. 24.

Diagnosis. A smooth species with a straight dorsal margin and rounded anterior and posterior margins; ventral margin sinuous-convex; median sulcus not well-developed; two short, strong spines.

Dimensions.	L	H
RV (MPK 11388)	0.56	0.29

Material. 11 specimens

Range in present study. A rare species, restricted to the Upper Campanian to Lower Maastrichtian in the outcrop samples. It shows a generally sporadic occurrence in the Upper Campanian basal *mucronata*, Eaton and Weybourne Chalks at Eaton, the Beeston Chalk at Caistor St Edmunds. It is also present in the higher samples of the Paramoudra Chalk of Whitlingham and appears again in the Pre-*Porosphaera* Beds of Sidestrand.

Bythoceratina sp. 4

Pl. 5, figs 25-26.

Diagnosis. A narrow, elongate species of *Bythoceratina* with a straight dorsal margin and a tapering posterior; anterior margin rounded with a marginal rib which is especially clear in LV. Ornament consists of a series of small, rounded tubercles, with a short postero-ventral spine and clear median sulcus.

Dimensions.	L	H
RV (MPK 11389)	0.49	0.21
LV (MPK 11390)	0.51	0.23

Material. 2 specimens

Range in present study. Restricted to the Upper Campanian in the outcrop samples. A single specimen was recovered from the Upper Campanian Middle Weybourne Chalk at Keswick (SAG 102) and the second individual came from the Paramoudra Chalk at Whitlingham (SAG 81).

Bythoceratina sp. 5.

Pl. 6, figs 2-3

Diagnosis. A medium species of *Bythoceratina* with a straight dorsal margin, a broadly rounded anterior margin and a narrow posterior; ventral margin strongly convex with a short postero-ventral spine; median sulcus long and deep. Ornament consists of a series of very small rounded tubercles.

Dimensions.	L	H
LV (MPK 11392)	0.46	0.25
RV (MPK 11393)	0.52	0.27

Depository. MPK 11392, 11393.

Material. 2 specimens

Range in present study. Restricted to the two top samples of the Upper Campanian Upper Weybourne Chalk (SAG 153, 154), Eaton. Specimens assigned to this species in the Lower Campanian *O. pilula* Zone are fragmentary and may not be conspecific.

Bythoceratina sp. 6

Pl. 6, figs 4-6.

Diagnosis. An elongate species of *Bythoceratina* with a straight dorsal margin, rounded, weakly dentate anterior margin and narrow oblique posterior; ventral margin straight to weakly convex. Median sulcus not strongly developed; postero-ventral spine broken; ornament consists of small, rounded tubercles.

Dimensions.	L	H
LV (MPK 11394)	0.55	0.23

Material. 4 specimens.

Range in present study. Restricted to the top sample (SAG 83) of the Paramoudra Chalk of Church Pit, Whitlingham.

Genus MONOCERATINA Roth, 1928

Treatise reference. Q268

Treatise diagnosis. "Typically elongate, with long straight dorsal margin terminating in caudal process; median sulcus extending near center of valve, commonly surrounded by crescentic lobe which may bear one or two thorn like spines." (See remarks below for slight amendment).

Remarks. Wilkinson (1988a, MS, p. 178) notes that the genus "was erected for Palaeozoic species and it is probably incorrect to assign most Mesozoic taxa to it. Many post-Palaeozoic species have been removed to other genera (e.g. *Bythoceratina)* but others, such as *M. longispina* are still retained."

Most authors continue to retain the *status quo* but *Monoceratina* should be used to accommodate only those forms with a single spine.

Monoceratina longispina (Bosquet, 1854)

Pl. 6, fig. 1

1854 *Cythere longispina* Bosquet, pl. 6, fig. 7a-d.
1941 *Monoceratina longispina* (Bosquet). Bonnema, pl. 6, figs 69-76.
1964. *Monoceratina* cf. *longispina* (Bosquet). Kaye, p. 53, pl. 3, fig. 1.
1965 *Monoceratina longispina* (Bosquet). Kaye, pl. 1, figs 3-7.
1968 *Monoceratina* cf. *bugensis* Szchzechura. King, MS, pl. 32, figs 7, 8.
1968 *Monoceratina longispina* (Bosquet). King, MS, pl. 35, figs, 7, 8.
1982 *Monoceratina longispina* (Bosquet). Weaver, p. 43, pl. 6, fig. 27.
1988a "*Monoceratina*" *longispina* (Bosquet). Wilkinson, MS, pl. 5, fig. 1.
1988b *Monoceratina longispina* (Bosquet). Wilkinson, pl. 1, fig. 1.

Diagnosis. A medium, smooth species of *Monoceratina* with a large, regularly conical and sharply pointed sub-alar spine. Distinct but delicate dorsal rib and two short horizontal ribs extending anteriorly from the base of the sub-alar spine and across the median sulcus. A short, pronounced, convex rib occurs on the ventral margin.

Dimensions.	L	H
LV (MPK 11391)	0.67	0.34

Depository. MPK 11391 and various assemblage slides

Material. 9 specimens.

Remarks. Morphologically, the closest species to *M. longispina* appears to be *Monoceratina parallela* Alexander, 1934, from the Santonian of Texas. The latter is slightly smaller and more strongly inflated. Kaye, 1964, considers it possible that "the two forms are synonymous with each other." If this was the case, *M. parallela* should be treated as a junior synonym of *M. longispina,* but the present author considers that they are not conspecific. Weaver (1982) places Bonnema's *M. longispina* in synonomy with *Bythoceratina umbonatoides* but refers the same figures also to *M. longispina* as they appear in the British Cenomanian. The current author retains them in the latter. King (MS, 1968, p. 309) includes Bosquet's species in synonymy with *M.* cf. *bugensis* of Szchzechura. The illustrated specimens are identical to the present material and are considered to be junior synonyms of *M. longispina*.

Published range. The species is relatively long ranging and is well documented in Britain. Kaye (1965) illustrates it from the Cambridge Greensand and from the Gault at Folkestone. King (MS, 1968) notes that the majority of his specimens were from the Upper Campanian Weybourne Chalk.

It is also recorded from the Cenomanian of Southern England and the Isle of Wight (Weaver, 1982); the Upper Chalk of Germany and Holland (Herrig, 1966) and the Maastrichtian of Denmark (Jorgenson, 1983). Wilkinson (1988a MS, 1988b) records the species from the Cenomanian of Eastern England, and from the Hunstanton Chalk member (1990).

Range in this study. In the outcrop assemblages, this species ranges from the Upper Campanian to Lower Maastrichtian. It is most common in the basal *mucronata* Chalk at Cringleford, but also appears in the Upper Weybourne Chalk at Eaton (SAG 152) and the Paramoudra Chalk at Whitlingham. It is less common in the Lower Maastrichtian and is restricted to the *O. lunata* Chalk of Trimingham.

Monoceratina montuosa (Jones & Hinde, 1890)

Pl. 7, figs 4-6.

1875 *Cythere (Cythereis) montuosa* Jones, p. 81-82 (*nomen nudum)*

1890 *Cytheropteron cuspidatum montuosum* Jones & Hinde, p. 38, figs 14-16.

1898 *Cytheropteron cuspidatum montuosum* Jones & Hinde. Chapman, p. 342.

1934 *Monoceratina montuosa* (Jones & Hinde). Alexander, p. 62, pl. 8, fig. 5.

1941 *Cytheropteron cuspidatum montuosa* (Jones & Hinde). Bonnema, p. 41, pl. 7, figs 1-9.

1958 *Monoceratina montuosa* (Jones & Hinde). Howe & Laurencich, p. 411.

1964 *Monoceratina montuosa* (Jones & Hinde). Benson & Tatro, pl. 2, figs 12, 15, 16.

1967 *Monoceratina* (sgen. n? 1) *montuosa* (Jones & Hinde) *montuosa*. Herrig, txt fig. 1, 2; pl. 1, figs 1-4.

1967 *Monoceratina* (sgen. n? 1) *montuosa* (Jones & Hinde) *vetula*. Herrig, text figs 1, 3, 4; pl. 1, figs 5-8.

1968 *Monoceratina cuspidata* (Jones & Hinde). King, MS, pl. 32, figs 9, 10.

1978 *Nemoceratina (Pariceratina) montuosa* (Jones & Hinde). Neale, pl. 14, figs 13, 14, 15, 16.

Diagnosis. A species of *Monoceratina* characterised by the presence of four tubercles on its dorsal margin, of which the second from the anterior is much the largest. There are two concave ribs, one on each side of the clear median sulcus. In LV, there is a large sub-alar spine, in RV, there is a similar but smaller spine immediately opposite on the anterior side of the median sulcus. Anteroventral and postero-ventral margin strongly denticulate.

Dimensions.	L	H
RV (MPK 11418)	0.70	0.35
RV (MPK 11419)	0.69	0.35
LV (MPK 11420)	0. 70	0.35
juvenile (SAG 216, Trunch Borehole)	0.63	0.28
adult (SAG 77, Paramoudra Chalk)	0.73	0.37

Depository. MPK 11418 - 11420

Material. At least 60 specimens

Remarks. The material of the present study is identical to that figured by Neale from the Chalk of Antrim, Northern Ireland, using Jones & Hinde's original specimens. Benson & Tatro (1963) record the species as a rare component of the Campanian Marlbrook Marl of Arkansas. Their figured specimen is reticulate,

whereas Howe & Laurencich (1958) state that, in Europe, the species is smooth. The American material is, nevertheless, included in synonomy with *M. montuosa* as being conspecific with the published records from Britain and Europe. The present material is quite similar to Benson and Tatro's specimens but the noding is stronger and more distinct. King (1968, MS) refers to the species as *M. cuspidata* but the illustrated material is identical to that of the present study and other authors who continue to use *M. montuosa* (Alexander, 1934 onwards, with the exception of Bonnema, 1941, who reverts to Jones & Hinde's original usage.) Neale (1978) refers the species to *Nemoceratina (Pariceratina).* The genus needs revision, but the present author has retained this species within *Monoceratina.* Herrig (1967) illustrates two subspecies *montuosa* and *vetula* from the Campanian of Rügen, which to the present author look remarkably similar, differentiated by size (the former subspecies larger than the latter). Both are here included in synonymy with Jones & Hinde's original species. It is possible that *M. montuosa vetula* is, at 0.64mm long, a late stage juvenile form of *M. montuosa montuosa(*adults 0.78, juveniles 0.60 mm in length).

Published range. In Britain, the range of this species is given (Neale, 1978, p. 360, table 5, p. 376) as Upper Campanian to Lower Maastrichtian. This range is also seen in Poland, Holland (Bonnema, 1941) and Rügen (Herrig, 1966). It was first recorded by Jones and Hinde from the Greensand (Aptian/Albian of England and the Chalk of Southern Antrim. It was recorded by Ross and Chimene (1982) from the Upper Taylor Group (=Campanian?) of central Texas. In an unpublished study of selected Ostracoda from the British Upper Chalk, King (1968, MS) gives a range for a conspecific species in Norfolk as extending from the upper *Gonioteuthis* Zone (Lower Campanian) to the Lower Maastrichtian.

It is also recorded from the Campanian of Texas (Alexander, 1934), the Marlbrook Marl of Arkansas (Benson & Tatro, 1964) and the Maastrichtian of Denmark (Jørgenson, 1978, 1983).

Range in this study. The species, as it occurs in the outcrop samples of this study, conforms to the previously published ranges of Neale and other authors, i. e. Upper Campanian to Lower Maastrichtian. The material of the Trunch Borehole exhibits an identical range to that of King (1968) i. e. uppermost Lower Campanian to Lower Maastrichtian but in keeping with Neale, 1978, the species is significantly more abundant in Upper Campanian samples.

It is rather sporadic in the basal *mucronata,* Eaton and Upper Weybourne Chalk at Eaton, occuring also in the Weybourne Chalk at Keswick. It is present in the Beeston Chalk at Caistor St Edmunds and was also seen in the lowest sample of Crown Point Pit (SAG 77) in the Paramoudra Chalk at Whitlingham. It also occurs higher up in the Paramoudra Chalk at Asylum Pit (SAG 112) and Tollgate Pit (SAG 111), Thorpe, near Norwich. It is less common in the Lower Maastrichtian, occurring in the *O. lunata* Chalk of Trimingham and the stratigraphically higher Pre-*Porosphaera* Beds at Sidestrand.

In the Trunch Borehole, the range is topmost Lower Campanian to Lower Maastrichtian; a slight extension to the published range of most other authors, but agreeing with King (1968, MS). The species is more common in the Upper Campanian and markedly more abundant than in the outcrop localities. Of the specimens studied, over 75% came from the Trunch Borehole. It first appears in the *Gonioteuthis quadrata* Zone (SAG 466, FAD) and extends up into the Lower Maastrichtian (SAG 216, LAD).

Monoceratina obvoluta Herrig, 1967.

Pl. 7, figs 1-3.

1967 *Monoceratina* (sgen. n? 1) *obvoluta* Herrig, pp. 208-210, text figs 1, 5, 6; pl. 2, figs 1-5.
1968 *Monoceratina paracuspidata* King, MS, pl. 35, figs 9-10.

Diagnosis. An ornate, medium and rather elongate species of *Monoceratina*, characterised by its ornament and denticulate margins; rounded anterior margin with 12 spines; ventral margin slightly spinose with a short, blunt postero-ventral spine. Dorsal margin straight, spinose with indistinct median sulcus. Posterior drawn out and truncate. Ornament finely reticulate across entire lateral surface.

Dimensions.	L	H
LV (MPK 11415)	0.60	0.25
LV (MPK 11416)	0.61	0.27
LV (MPK 11417)	0.60	0.25

Depository. MPK 11418-11420.

Material.. 18 specimens.

Remarks. The present material is identical to Herrig's material from the Schreibkreide of Germany in size, shape and range (type level Lower Campanian). It is extremely rare in published records; the present author has not found any other references. King's (1968, MS) unpublished *Monoceratina paracuspidata* is here considered synonymous with Herrig's *M. obvoluta* and the material of the present study, as the illustrated specimens are identical.

Range in this study. Lower Campanian to Lower Maastrichtian.

In the Trunch Borehole, the species first appears in the *Gonioteuthis quadrata* Zone of the Lower Campanian (FAD SAG 462) and disappears in the *B. lanceolata* Zone of the Lower Maastrichtian. In the outcrop samples, it is very rare, restricted to a single sample from the Upper Campanian Eaton Chalk (SAG 96) at Eaton, and one sample (SAG 2007) from the Lower Maastrichtian Grey Beds at Trimingham.

Monoceratina pedata pedata (Marsson, 1880).

Pl. 6, figs 18, 20-23.

1880 *Cythere pedata* Marsson, p. 46, pl. 13, fig. 16a.
non. Cythere pedata Geinitz, 1845, p. 46.
1890 *Cytheropteron pedatum* Marsson. Jones & Hinde, p. 38, pl. 4, figs 33-35.
1929 *Cytherura spooneri* Israelsky, p. 6.
1933 *Monoceratina pedata* (Marsson). Alexander, p. 203, pl. 27, fig. 15a-b.
1934 *Monoceratina pedata* (Marsson). Alexander, p. 60.
1936 *Monoceratina pedata* (Marsson). Van Veen, p. 42.
1941 *Monoceratina pedata* (Marsson). Bonnema, p. 29, pl. 6, figs 27-30.
1946. *Monoceratina pedata* (Marsson). Van den Bold, pl. 14, fig. 8.
1948. *Monoceratina pedata* (Marsson). Schmidt, p. 411, pl. 61, fig. 10.
1957. *Monoceratina pedata* (Marsson). Butler & Jones, p. 24, pl. 24, fig. 3.
1958 *Monoceratina pedata* (Marsson). Howe & Laurencich, p. 415.
1963 *Monoceratina marssonitina* nom. nov. Coryell, p. 1019.
1964 *Monoceratina pedata pedata* (Marsson). Kaye. p. 54, pl. 3, fig. 9-14.
1964 *Monoceratina marssonitina* Coryell. Benson & Tatro, pl. 2, fig. 13, 14.
1965 *Bythoceratina (Monoceratina) pedata* (Marsson). Damotte, p. 322, pl. 6, fig. 4.

1966 *Monoceratina* (s. gen. n. 1?) *pedata* (Marsson). Herrig, p. 901-4, pl. 38, figs 6-9.

1968 *Monoceratina marssonitina* Coryell. King, MS, pl. 33, fig. 8; pl. 34, figs 1, 2, 5.

1971 *Monoceratina pedata* (Marsson). Damotte, pl. 6, fig. 11.

1980 *Monoceratina pedata* (Marsson). Babinot, p. 77-78, pl. 4, fig. 5.

1985 *Cuneoceratina* cf. *pedata* (Marsson). Babinot *et al.*, pl. 56, fig. 11.

1988 *Cuneoceratina pedata* (Marsson). Bless, pl. 2, fig. G.

1992 *Cuneoceratina pedata* (Marsson). Puckett, p. 185-6, fig. 58.9

Diagnosis. A large species, distinguished by its tapered postero-dorsal caudal process and obliquely rounded anterior; a prominent marginal rim on the lower two-thirds; dentate margins with promonent rim; ornament strongly reticulate. Numerous short spines arise from the union of the reticulate ridges. Strong postero-ventral, slightly backwardly directed spine.

Dimensions.	L	H
RV (MPK 11410)	0.86	0.39
LV (MPK 11411)	0.83	0.37

Depository. MPK 11410-11414

Material. More than 100 specimens.

Remarks. In the diverse ostracod fauna of the Danish Maastrichtian White Chalk, only species of the genus *Bythoceratina* (including species now assigned to *Monoceratina)* show a significant geographical and stratigraphical variation. A biostratigraphical subdivision has been established on the basis of this (Jørgenson, 1978, 1982, 1983) and *Monoceratina pedata* seems to be particularly useful. In the material of the present study, there are many broken specimens of this species. The lateral spines are particularly prone to damage but some complete specimens were recovered. The shape of the carapace is distinctly inflated and the backward facing spine is pronounced, as can be seen in illustrated specimens. Israelsky (1929) described *C. spooneri* from the middle Campanian Marlbrook Marl of Texas; this species is considered to be conspecific with *M. pedata* and is included as such in its synonymy. Later authors (e.g. Babinot *et al.,* 1985; Bless, 1988, Puckett, 1992) assign the species to *Cuneoceratina* but the present author prefers *Monoceratina*. The use of *M. marssonitina* by authors post-1963 is not considered to be justified and all references to this new name are included in synonymy with *M. pedata*.

King (MS, 1968, p. 322) lists a synonymy for *M. marsonitina* which, although including many references to *M. pedata,* also treats Jones & Hinde's material as not conspecific, along with Bold, 1946; Kaye, 1964 and Benson & Tatro, 1964. King's material is, however, identical in size and shape, but is slightly smaller. This is a species which needs some revision or taxonomic work to determine whether it does belong to *Monoceratina* or *Cuneoceratina.*

Stratigraphical range and distribution.

Babinot *at al.,* 1985, notes that this is a "classic species throughout the Senonian of Northern Europe." The published range is Turonian to Lower Maastrichtian. King, 1968, MS, recorded the species from the Lower Campanian upper *Gonioteuthis* Zone and Upper Campanian lower *mucronata* Zone in Norfolk. The range in the present study is significantly less restricted.

Upper Cretaceous, USA, (Alexander, 1933, 1934)

Turonian to Santonian: Provence (Babinot, 1980),

Upper Santonian: France (Babinot, *et al.*, 1985).

Campanian: middle Campanian Marlbrook Marl of Texas (Israelsky, 1929); Lower Campanian Ozan and Anona Chalks and the Upper Campanian Saratoga Chalks of Louisiana (Butler & Jones, 1958); Upper Campanian, Paris Basin (Damotte, 1971a; Babinot *et al.,* 1983), Southern Belgium (Bless, 1988)
Campanian to Maastrichtian; Demopolis Chalk (Puckett, 1992)
Maastrichtian: Lower Maastrichtian of Poland, Germany (Herrig, 1966) and Denmark (Jørgenson, 1983).
Range in this study. Coniacian to Lower Maastrichtian in outcrop assemblages; Lower Campanian to Lower Maastrichtian in the Trunch Borehole.

In the outcrop samples, it first appears in the topmost basal *coranguinum* Zone of the Coniacian, passing through the low *coranguinum* Zone and *coranguinum* Zones of Norfolk and Suffolk. It is absent in the Santonian and Lower Campanian, appearing again in the Upper Campanian of Stoke Holy Cross, Catton Grove and Keswick. It occurs in all samples of the basal *mucronata* and Eaton Chalk horizons at Cringleford. At Eaton, it also occurs in most samples from the basal *mucronata* Chalk, through the Eaton Chalk and up into the Upper Weybourne Chalk. It is found in the lower samples of the Beeston Chalk at Caistor St Edmunds but disappears in the upper samples (SAG 53-58). It is present in most of the Paramoudra Chalk at Whitlingham and is also found in the Lower Maastrichtian *O. lunata* Chalk and Grey Beds of Trimingham and the Pre-*Porosphaera* Beds of Sidestrand.

In the Trunch Borehole, the species shows a similar range, first appearing in the lower *O. pilula* Zone of the Lower Campanian (FAD SAG 626). The species also appears in the G. quadrata Zone, but is rather sporadic. It is more abundant in the Upper Campanian, where it occurs as an almost ubiquitous component in Zone/subdivision 10-14. It crosses the Campanian - Maastrichtian Boundary and extends up into the top sample of the Lower Maastrichtian (SAG 213).

Monoceratina pedata laevoides (Marsson, 1880)

Pl. 6, figs 15-17, 19.

1880 *Cythere pedata laevoides* Marsson, p. 45, pl. 3, fig. 16a-c.
1941 *Monoceratina laevoides* Bonnema, p. 29, pl. 6, figs 47-53.
1958. *Monoceratina laevoides* (Bonnema). Howe & Laurencich, p. 410.
?1964. *Monoceratina* cf. *pedata laevoides* (Bonnema). Kaye, p. 55, pl. 3, fig. 17.

Diagnosis. A smooth sub-species with a clear median sulcus, identical in shape to the nominative species; small tubercles scattered over surface, especially dorsally and in a line below the large lateral spine.

Dimensions.	L	H
RV (MPK 11404)	0.85	0.34
LV (MPK 11409)	0.81	0.32

Depository. MPK 11404-11409 and species slide 20.
Material. 16 specimens.
Remarks. Kaye's figured specimen is, at 0.96 mm in length, larger than the specimens seen in the present study. The subspecies itself is very similar to *M. pedata pedata*, but can be distinguished by the lack of reticulation on the lateral surface. Kaye suggests that the close association and similarity between the two subspecies indicates that *M. pedata laevoides* could be an extreme variant of *M. pedata pedata*. However, many authors consider the two forms as separate sub-species and this is followed in the

present study. It should be noted that the small tubercles seen in the described specimens, whether by preservation or morphological variation, are not always evident in other specimens

Stratigraphical range and distribution. Jones & Hinde record the species from the Chalk of Dunstable. Bonnema describes it from the Upper Cretaceous Chalk of the Netherlands, while Kaye (1964) in a revision of Jones and Hinde's material, illustrates a related subspecies (placed in synonomy in this study) from the Upper Chalk of Norwich; Jørgenson (1983), Maastrichtian White Chalk of Denmark.

Range in this study. Upper Campanian to Lower Maastrichtian.

In the Trunch Borehole, this subspecies has a more restricted range than *M. pedata pedata*. It first appears just above the Lower Campanian – Upper Campanian boundary (SAG 433, first appearance, basal *mucronata* Zone) and is rather sporadic throughout its entire range. It disappears in the Lower Maastrichtian *B. lanceolata* Zone (SAG 217, last appearance). In the outcrop assemblages, it is restricted to the Lower Maastrichtian *O. lunata* Chalk of Trimingham and the stratigraphically higher Pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand.

Genus NEMOCERATINA Gründel & Kozur, 1971

Subgenus PARICERATINA Gründel & Kozur, 1971

Weaver (1982, p. 44) gives the diagnoses of both genus and subgenus.

Nemoceratina (Pariceratina) tricuspidata (Jones & Hinde, 1890)

Pl. 7, fig. 7.

1890 *Cytheropteron cuspidatum tricuspidatum* Jones & Hinde, pl. 3, figs 6-7.

1936 *Cytheropteron cuspidatum tricuspidatum* Jones & Hinde. Van Veen, p. 43.

1936. *Monoceratina tricuspidata* (Jones & Hinde). Van Veen, p. 42, pl. 2, figs 4-11.

1941 *Monoceratina tricuspidata* (Jones & Hinde). Bonnema, pl. 6, fig 77-80.

1941 *Monoceratina tricuspidata* (Jones & Hinde). Triebel, p. 353.

1958 *Monoceratina tricuspidata* (Jones & Hinde).Howe & Laurencich, p. 422.

1964 *Monoceratina tricuspidata* (Jones & Hinde). Kaye, pl. 3. figs 7, 8, p. 56.

1968 *Monoceratina tricuspidata* (Jones & Hinde). King, MS, p. 340, pl. 37, fig. 2.

1978 *Nemoceratina (Paraceratina) tricuspidata* (Jones & Hinde). Neale, pl. 14, figs 7-8.

1982 *Nemoceratina (Paraceratina) tricuspidata* (Jones & Hinde). Weaver, pl. 7, figs 14-16.

1988 *Nemoceratina (Paraceratina) tricuspidata* (Jones & Hinde). Wilkinson, MS, pl. 1, fig. 8

Diagnosis. A fragile and thin shelled species of *Nemoceratina (Paraceratina)* with three strong ventral spines ; surface reticulate above two posterior spines. Median sulcus broad, extending between the two anterior spines.

Dimensions.	L	H
(MPK 11421)	0. 60	0.31

Depository. MPK 11421 and various assemblage slides.

Material. At least 10 specimens.

Remarks. A very rare species in published records, originally assigned to *Monoceratina* (Van Veen, Bonnema, Triebel, Howe & Laurencich, Kaye) but placed in *Nemoceratina (Pariceratina)* by later authors

following the erection of Grũndel & Kozur's new genus in 1971 (e.g. Neale, Weaver, Wilkinson). Certainly, it could not be retained in *Monoceratina* due to its three spines. It is very fragile and may well be destroyed during processing. This might account for the sporadic and sparse record. The present material is very close to published illustrated specimens, especially those of Weaver, 1982, from the British Upper Cenomanian, King, 1968, MS, and Neale, 1978. The form described by Keij, 1957, as *M. tricuspidata* is considerably more elongate and bears four lateral spines; it is, therefore, not considered conspecific.

Stratigraphical range and distrubution. In the British record, this species ranges from Santonian to Maastrichtian (Kaye, 1964), but Wilkinson (1988) has extended this range back to the Cambridge Greensand of eastern England. Weaver also records it from the Cenomanian. It is also known from the Albian to Coniacian and Lower Chalk of Germany (Babinot *et al.*, 1981, Herrig 1965) and the Upper Chalk of Holland (Bonnema). It is also known from the Lower Maastrichtian of Rügen (Herrig, 1966).

Range in this study. Extremely rare in the present study and not seen in the Lower Maastrichtian or the Coniacian to Lower Campanian part of its range. In the Trunch Borehole, it is restricted to the Upper Campanian Weybourne Chalk, Beeston Chalk and Paramoudra Chalk horizons, first appearing at SAG 372 and extending up to the Campanian – Maastrichtian boundary (LAD SAG 241). It does not occur above this level.

In the outcrop samples, it occurs in the upper samples of the Beeston Chalk, Caistor St Edmund and in a single sample from the Paramoudra Chalk of Crown Point Pit, Whitlingham.

Genus PATELLACYTHERE Gründel & Kozur, 1971

Diagnosis. Weaver, 1982, p. 44 "outline subrectangular to rounded. Surface smooth to pitted; lateral spine reduced to a broad swelling. There is often a weak dorsal rib. Hinge of LV with smooth median bar."

?Patellacythere sp. cf. sp. A (of Weaver,1982)

Pl. 7, fig. 8.

cf 1982 *Patellacythere* sp. A, Weaver. p. 45, pl. 7, figs 11-13.

Diagnosis Thin-shelled, broken specimen, ventral margin straight at anterior, then convex, curving up sharply to posterior. Posterior rounded, anterior margin broadly rounded, without marginal rib. Ventrolateral spine very short, median sulcus broad.

Dimensions	L	H
RV (MPK 11422)	0.49	0.22

Material 1 specimen

Remarks Very similar to Weaver's *Patellacythere* sp. A from the British Cenomanian and can possibly be referred to this species. It is, however, left in open nomenclature due to its extreme rarity.

Range in this study. This species is restricted to a single sample from the Upper Campanian Paramoudra Chalk at Asylum Pit, Thorpe, near Norwich (SAG 112).

Genus CUNEOCERATINA Gründel & Kozur, 1971

Cuneoceratina salebrosa (Jones & Hinde, 1890)

Pl. 7, fig. 10

1890 *Cytheropteron pedatum salebrosa* Jones & Hinde, pl. fig. 8, pl. 4, fig. 32.

1964 *Monoceratina pedata salebrosa* (Jones & Hinde). Kaye, pl. 3, figs 15, 16.

1978 *Cuneoceratina salebrosa* (Jones & Hinde). Neale, pl. 14, figs 9-12.

Diagnosis Carapace large, flattened and rather wedge shaped; anterior margin extremely broadly rounded, posterior narrow; small tubercles on lateral surface with a row below the broken lateral spine.

Dimensions	L	H
RV (MPK 11423)	0.80	0.43

Material 12 specimens

Remarks. The present material is smaller than Jones & Hinde's specimens from the Chalk of Northern Ireland. It is also slightly smaller and less ornate than ?*Cuneoceratina* sp. of this study with a weaker ventral rib. The lateral surface is smooth, whereas ?*Cuneoceratina* has large round pits.

Kaye (1964) states that his specimens of *M. pedata salebrosa* are "very closely related to *M. pedata pedata*, differing principally in the surface ornament. However, if plate 3 is examined, while there is a superficial resemblance, the two species, in the opinion of the present author, belong in different genera. *M. pedata salebrosa* is not a subspecies of *M. pedata pedata.* The present author follows such authors as Neale (1978) in assigning the present material to the genus *Cuneoceratina*. The latter specimens, figured by Neale as *C. salebrosa* very closely resemble those of Kaye. In both figures, the short lateral spine, so obvious in *M. pedata pedata* is not seen.

Range in this study. The species has a published range of Campanian and Lower Maastrichtian, but in this study it is restricted and sporadic in its occurrence. It is present in the Upper Campanian basal *mucronata* Chalk at Cringleford and Eaton and in the Beeston Chalk of the Trunch Borehole. In the Lower Maastrichtian, it is a rare in the *O. lunata* Chalk at Trimingham, and is slightly more common in the Pre-*Porosphaera* Beds of Sidestrand.

?Cuneoceratina sp.

(not illustrated)

Diagnosis. A rather large species, anterior margin very broadly rounded, posterior narrow. Ventral rib strongly developed; surface ornament consisting of deep, rounded pits.

Dimensions.	L	H
SAG 345	0.72	0.36

Depository. Assemblage slide SAG 345.

Material. 1 specimen

Range in this study Restricted to a single sample (SAG 345) from the Upper Campanian Beeston Chalk of the Trunch Borehole; not seen in the outcrop samples.

Genus CRASSACYTHERE Gründel & Kozur, 1972.

Crassacythere sherborni (Jones & Hinde, 1890)

Pl. 6, figs 7-14.

1890 *Cytheropteron sherborni* Jones & Hinde, pl. 1, figs 33, 34; pl. 4, figs 20, 21.

1958 *Cytheropteron sherborni* Jones & Hinde. Howe & Laurencich, p. 306.

1964 *Monoceratina sherborni* (Jones & Hinde). Kaye, pl. 2, fig. 4.

1968 *Monoceratina sherborni* (Jones & Hinde). King, MS, pp 334 - 336, pl. 36, figs 5-6.

1978 *Crassacythere sherborni* (Jones & Hinde). Neale, pl. 15, figs 1-4.

Diagnosis. A large, tumid, subrectangular species with a well-developed, deep median sulcus; ornament consists of strongly developed concentric ribbing with small rounded tubercles. Anterior margin broadly rounded, posterior more narrowly rounded, dorsal margin straight.

Dimensions.	L	H
RV (MPK 11399)	0.78	0.50
RV (MPK 11400)	0.75	0.45
LV (MPK 11401)	0.75	0.45

Material. At least 30 specimens.

Remarks. *Monoceratina crassa* Szczechura, 1964, is a more strongly ornamented species with a broader posterior margin. *M. flata* Szczechura, 1964, is similar in shape, but differs in ornament and its weaker median sulcus and stronger postero-ventral bulge.

Published range. Both King (1968, MS) and Neale, 1978, state that this species occurs in the Upper Campanian and Lower Maastrichtian in Britain. The present material is very similar to previously illustrated specimens but is more restricted in its stratigraphical range.

Range in this study. In the outcrop assemblages, the species is sporadic in occurrence. It first appears in the low *coranguinum* Zone of the Coniacian, but is absent in the higher Coniacian and Santonian high *coranguinum*, *Uintacrinus* and *Marsupites testudinarius* zones (2, 3, 4). It does not appear in the Lower Campanian and is present only in the lower horizons of the Upper Campanian (Zone/subdivision 10, basal *mucronata* Chalk of Eaton and Cringleford). In the Trunch Borehole, the species appears immediately below the Lower Campanian - Upper Campanian boundary (FAD SAG 433) and extends up to a few samples below the Campanian-Maastrichtian boundary (LAD SAG 277, Paramoudra Chalk).

Genus PSEUDOCYTHERE Sars, 1866.

Treatise reference. Q 268

Treatise diagnosis. "Carapace compressed, without lateral expansions; caudal process continuous with dorsal margin; no median sulcus, duplicature broad."

?Pseudocythere sp.

Pl. 7, figs 9, 11-13.

Diagnosis. A small, elongate, sub-ovate species with an anterior rib parallel to the margin; rounded anterior and posterior margins. Dorsal and ventral margins straight and almost parallel. Ornament consists of a series of straight, narrow ribs which only extend halfway across the posterior two-thirds of the lateral surface, anterior part of valve smooth.

Dimensions.	L	H
LV (MPK 11424)	0.34	0.14
LV (MPK 11425)	0.36	0.17
RV (MPK 11426)	0.36	0.16

Material. 7 specimens.

Remarks. The small size and fragile nature of this species means that it is easily overlooked, which might explain its sparse record. It is probably new ; it is certainly distinctive and the present author has seen nothing like it in published works. It was, however, left in open nomenclature due to its sparse record, as questionably belonging to *Pseudocythere,* until its exact generic identity can be determined. This is currently uncertain due to the poor preservation of the hinge and internal details such as muscle scars and inner lamellae.

Weaver, 1982 (p. 36, pl. 15, figs 15, 16) illustrates specimens of *Cytherura? striatoides* Bonnema, 1941 (previously figured by Herrig, 1966, and King, 1968, MS). It was only tentatively referred to *Cytherura* because "there are some differences beween it and other *Cytherura* species. Firstly species of *Cytherura* have a distinctive caudal process; *C. striatoides* has a drawn out posterior , but no caudal process as such; in addition it is subtriangular in outline not subreniform and possesses small anterior and posterior vestibules which are not seen in *Cytherura* species. C. striatoides may, therefore, belong to a new genus and it is only tentatively referred to *Cytherura."* King (MS, 1968, pl. 8, figs 7, 8, 10) illustrates three "form-types"; the first of which is identical to that of Bonnema, Herrig and Weaver; the third from the Lower Maastrichtian of Norfolk exhibits weaker striation.

The present material differs from *C? striatoides* in its shape (less triangular with rounded anterior and posterior margins) and the ornament only covers the posterior two-thirds of the valve, while in both Weaver & King's material, the ornament extends across the entire lateral surface, with the exception of King's form 3. In this "form-type", the valve is less triangular and general ornament is closer to the present material. Indeed, King raises the possibility that form 3 is new. However, the relationship of these forms is doubtful and they may simply be due to sexual dimorphism with form 1 representing males and form 3 females. It might have been possible to erect a new species based on the present material and King's form 3, but this would require a detailed examination of the original type material of Bonnema and also that of Herrig, King and Weaver. This was considered to be beyond the scope of this thesis and so the species was left in open nomenclature, tentatively referred to the genus *Pseudocythere.*

Range in this study. The species first appears in the higher *coranguinum* Zone (3) of the Coniacian in the assemblages of South Pickenham, appearing again in the Upper Campanian basal *mucronata* Zone

(zone/subdivision 10) and the Lower Maastrichtian Grey Beds of Trimingham (zone/subdivision 18). In the Trunch Borehole, it is also sporadic, occurring as rare components of assemblages in the Upper Campanian Beeston and Paramoudra chalks (zone/subdivision 13, 14).

Family CYTHERIDAE

Genus SAIDA Hornibrook, 1952.

Treatise reference. Q 356

Treatise diagnosis." Minute, subrhomboidal; ventrolateral margins expanded to form blunt processes rather similar to *Cytheropteron*; hinge consisting of 2 simple teeth in RV separated by straight, simple groove; LV with terminal sockets and horizontal, straight, simple bar between; caudal process absent; muscle scar pattern consisting of four elongate scars, one above other with a single scar in front; radial canals simple, not numerous; line of concrescence coinciding with inner margin; duplicatures wide."

Remarks. The range given in the *Treatise* is Eocene to Recent but several Cretaceous species have since been erected. This genus has been previously left by many authors (e. g. *Treatise*, 1961; King, MS, 1968, p. 358) as Uncertain but is now included in the Cytheridae.

Saida prasutegusi sp. nov.

Pl. 7, figs 14-18.

Derivatio nominis: Reflects the type locality of this species; after Prasutegus, the king of the Iceni, the Iron Age tribe in East Anglia at the time of the Roman invasion.

Holotype. Female RV (MPK 11428)

Type level. *O. lunata* Chalk.

Type locality. Sidestrand, Norfolk.

Diagnosis. A small species; sub-rhomboidal to sub-ovate, with an arched dorsal margin, rounded anterior and posterior margins; narrow, smooth marginal rim, ventrolateral margin expanded to form a blunt alar process. Distinguishable from other Cretaceous species by its ornament.

Description. Small, relatively thin shelled; subrhomboidal to sub-ovate, with an arched dorsal margin in LV, almost straight in RV, LV slightly larger than RV; apex at mid-length, rounded anterior (more so in LV) and posterior margins, greatest height at mid-height, posterior slightly flattened in lateral view; ventro-lateral margin expanded to form a blunt alar process which does not obscure the ventral margin in lateral view; no sub-central tubercle and no ocular tubercle or internal ocular sinus. Males more elongate and less inflated than females; no juveniles. Ornament covers entire lateral surface, including the ventro-lateral process, except for the smooth narrow rim along the anterior, posterior and ventral margins, especially prominent at anterior. Ornament consists of small, round, regularly spaced puncta.

Antimerodont hinge feebly developed or poorly preserved, in RV consists of dentate terminal bars separated by a straight locellate groove. Marginal zone moderately wide; avestibulate; muscle scars not seen; radial canals simple, not numerous.

Dimensions.	L	H
Holotype, female RV (MPK 11428)	0.35	0.24
Paratype, female RV (MPK 11429)	0.33	0.24
Paratype, male LV (MPK 11430)	0.41	0.22
Paratype, female LV (MPK 11431)	0.35	0.25
Paratype, female LV (MPK 11432)	0.33	0.26

Depository. MPK 11428-11432.

Materal. 12 specimens.

Remarks. *Saida* species have only been rarely recorded from the Cretaceous, possibly because of their small size and fragile, thin-shelled carapaces; they are easily destroyed during sample processing or subsequent picking. The present material differs from King's (1968, MS) unpublished *Saida linguata* in ornament (more regularly pitted, although the holotype appears almost smooth in the illustrated figures). The species is, however, very similar in size and shape. *Saida marginopunctata* Symmonds (1996, MS, pl. 4, figs 4-8), from the Lower Albian of Morocco is a larger species with a similar ornament but with fine marginal punctae. *Saida elliptica* (Bonnema, 1941) has a similar ornament but the present species is larger and more ovate, with a more rounded dorsal margin in the LV, the ventrolateral process is also more pronounced. *Saida nettgauensis* Grŭndel, 1966, from the Lower Albian of Germany (p. 49, pl. 8, figs 36, 37) is larger, with longer, more ventrally positioned lateral rib. *S.* cf. *S. nettgauensis* of Weaver, 1982 (p. 98, pl. 20, figs 4, 5, 6) from the British Middle and Upper Cenomanian, can be distinguishedby its coarser reticulation, more angular ventrolateral rib and ventrolateral spine.

Range in this study. The species is rare in the Upper Chalk of East Anglia. In the outcrop samples, it is restricted to the Upper Campanian Paramoudra Chalk (14) and the Lower Maastrichtian pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand and the *O. lunata* Chalk of Trimingham (zone/subdivisions 15-17). In the Trunch Borehole, it occurs in the Paramoudra Chalk and in the Porosphaera Beds.

Family CYTHERIDEIDAE Sars, 1925.

Subfamily CYTHERIDEINAE Sars, 1925.

Genus ASCIOCYTHERE Swain, 1952.

Treatise reference. Q 273

Treatise diagnosis. "Carapace plump, sub-ovate; LV with crenulate terminal sockets separated by a smooth median bar, above which is a well defined accommodation groove. Marginal areas narrow, with numerous radial canals."

Remarks. The Cytherideinae are discussed in detail in the final section of chapter 1 of this thesis, with special reference to hinge morphology and evolution (figs 1.26, 1.27a, 1.27b, 1.27c, 1.27d.

Asciocythere hadratos sp. nov.

Pl. 8, figs 5, 7, 9-13; pl. 9, figs 2-5.

Derivatio nominis. Gr. αδρος - hadros - with reference to the thick-shelled carapace of this species.

Holotype. LV (MPK 11440)

Type level. Upper Campanian Paramoudra Chalk.

Type locality. Crown Point Pit, Whitlingham, Norfolk.

Diagnosis. A thick shelled species; sub-ovate, often with a rough surface but sometimes smooth due to differential preservation, characterised by broadly rounded, smooth or feebly dentate anterior and a smooth posterior margins; dorsal margin highly arched dorsal margin.

Description. Medium. Subovate. Thick shelled. Anterior margin very broadly rounded with 5 minute marginal denticles. Posterior margin more narrowly rounded. Both margins with apex below mid-height. Dorsal margin sub-umbonate with apex at mid-length. Ventral margingently convex in lateral view, with oral incurvature in internal view. LV strongly overlaps RV. Smooth. Inner lamella strongly calcified; rather narrow for genus. Radial pore canals poorly seen but relatively numerous and in fan shaped arrangement. Hinge antimerodont with, in the LV, loculate terminal sockets, with 6 loculi anteriorly and 5 posteriorly, separated by a denticulate bar. A gutter-like accommodation groove occurs above the median element in the LV. Muscle scars not seen.

Dimensions.	L	H
Holotype LV (MPK 11440)	0.66	0.42
Paratype RV (MPK 11439)	0.63	0.40
Paratype LV (MPK 11441)	0.63	0.41
Paratype LV (MPK 11443)	0.66	0.44
Paratype LV (MPK 11438)	0.66	0.43
Paratype LV (MPK 11444)	0.65	0.43
Paratype LV (MPK 11447)	0.67	0.45

Material. Over 100 specimens.

Remarks. *Clithrocytheridea* aff. *C. brevis* (Cornuel, 1946) from the French Lower Albian to Aptian (Oertli, 1958, pl. 4, figs 87-89) is a variable species with the female RV resembling *A. prionodes* sp. nov., but smaller and less posteriorly elongate, and the LV of both sexes more like *A. hadratos* sp. nov. (but smaller). *Clithrocytheridea* aff. *C. brevis* is more strongly dimorphic than the material of the present study, with males (Oertli, 1958, pl. 4, figs 89, 94-99) more elongate than females (1958, pl. 4, figs 87, 90-93). *Asciocythere rotunda* (Vanderpool) as illustrated by Swain & Chuanli, 1991, is similar in shape but less heavily calcified and smaller. Gründel, 1974 (pl. 3, figs 13-16) illustrates *Asciocythere (Stravia) bonnemai*

from the Santonian of Austria, which is very similar in shape to the present species but is smaller and more dimorphic.

Range in this study. In the Trunch Borehole, the species ranges from the middle of the Lower Campanian *Gonioteuthis quadrata* Zone (9, FAD SAG 540) into the Lower Maastrichtian. In the outcrop samples, it first appears in the Coniacian *coranguinum* Zone (3), but is a Lazarus taxa across the Santonian and early to middle part of the Lower Campanian, reappearing in the *Gonioteuthis quadrata* Zone (9) and is then present in zone/subdivisions 10-14 (basal *mucronata* Chalk, Eaton Chalk, Weybourne Chalk, Beeston and Paramoudra chalks and in the Lower Maastrichtian pre-*Porosphaera, Porosphaera, O. lunata* and Grey Beds of Sidestrand and Trimingham (zone/subdivisions 15-18).

Asciocythere margieri Babinot, 1980.

PL. 8, fig. 4.

1980 *Asciocythere margieri* Babinot, pp 79-81, pl. 4, figs 9-14.

1983 *Asciocythere margieri* Babinot. Babinot & Colin, fig. 8H, J.

1985 *Asciocythere margieri* Babinot. Babinot *et al.*, pl. 56, figs 3-5.

Diagnosis. A small species of *Asciocythere* with depressed anterior and posterior areas; ventral margin strongly convex; anterior and posterior margins moderately broadly rounded; highest at mid-point and valve appears rather tumid. Ornament finely punctate, covering entire lateral surface.

Dimensions.	L	H
LV (MPK 11437)	0.43	0.30

Depository. MPK 11437

Material. 1 specimen.

Remarks. Slightly more elongate and larger than Babinot's *A. margieri*, but probably conspecific or very closely related (Babinot's specimens - 0.40mm in length; present material 0.43mm). It is similar in shape to *A. hadratos* sp. nov. but differs in ornament; the latter being smooth and more heavily calcified. It is also smaller and more elongate.

Published range. Babinot first recorded the species from the Upper Turonian of France. Babinot & Colin (1983) also record it from the French Late Turonian.

Range in this study. Restricted in the present study to a single sample (SAG 17) from the Coniacian low *coranguinum* Zone (2) at Euston, Suffolk.

Asciocythere prionodes sp. nov.

PL. 8, figs 14-22; pl. 9, fig. 1.

Derivatio nominis. Gr. πριονωδηξ prionodes -saw-like, with reference to the very small anteroventral marginal denticles seen in the LV of this species.

Holotype. LV MPK 11459

Type level. Upper Campanian basal mucronata Chalk.

Type locality. Cringleford, Norfolk.

Diagnosis. A sub-ovate (LV) to sub-triangular (RV) species, with denticles on the antero-ventral margin, especially of the LV, which resemble a saw blade; dorsal margin strongly arched in LV, less so in RV.

Description. Medium. Rather thin-shelled for the genus. Elongate-subovate in LV to rounded sub-triangular in RV. Anterior margin asymmetrically rounded with apex below mid-height and bearing, anteroventrally and especially in LV, a number of small marginal denticles which impart a serrated, saw-like aspect to the margin. Dorsal margin strongly covex about apex which is just anterior of mid-length. Ventral margin straight to gently convex in lateral view. LV > RV with overlap around entire periphery. Smooth. Inner lamella relatively wide. Hinge antimerodont, with gutter-like accommodation groove above the median element in the LV. Muscle scars a vertical row of four adjacent oval scars, with a heart shaped frontal scar.

Dimensions.	L	H
Holotype LV (MPK 11459)	0.65	0.41
Paratype RV (MPK 11451)	0.57	0.37
Paratype RV (MPK 11452)	0.58	0.37
Paratype RV (MPK 11453)	0.60	0.39
Paratype RV (MPK 11454)	0.60	0.39
Paratype RV (MPK 11455)	0.57	0.36
Paratype LV (MPK 11456)	0.61	0.39
Paratype RV juv. A1? (MPK 11457)	0.54	0.35
Paratype LV (MPK 11458)	0.61	0.39

Depository. MPK 11451-11459.

Material. More than 80 specimens.

Remarks. *Clithrocytheridea parva* Weaver, 1982, (p. 32, pl. 5, figs 14-17), from the British Lower Cenomanian is similar in shape, but is significantly smaller; the posterior is also more broadly rounded and the dorsal margin more strongly arched. Witte *et al.*, 1992 (pl. 3, figs 2-3) illustrates Weaver's species from the Lower Cenomanian of the eastern Netherlands, which also differs from *A. prionodes*. *Clithrocytheridea* aff. *C. brevis* (Cornuel, 1946) from the French Lower Albian to Aptian (Oertli, 1958, pl. 4, figs 87-89) is a variable species with the female RV resembling *A. prionodes* sp. nov., but smaller and less posteriorly elongate, and the LV of both sexes more like *A. hadratos* sp. nov. (but smaller).

Range in this study. In the Trunch Borehole, the species ranges from the mid-Lower Campanian *G. quadrata* Zone (9) (FAD - SAG 540) into the Lower Maastrichtian *B. lanceolata* Zone. A similar range is also seen in the outcrop samples.

Asciocythere sp. 1.

Pl. 8, figs 1-3, 8.

Diagnosis. A medium, sub-ovate species of *Asciocythere* with an arched dorsal margin and a broadly rounded anterior margin.

Dimensions.	L	H
LV (MPK 11433)	0.48	0.33

Depository. MPK 11433-11436

Material. 6 specimens

Range in this study. In the outcrop samples, the species first appears in the Coniacian low *coranguinum* and *coranguinum* zones (2 and 3) but is a Lazarus taxa throughout the Santonian and earlier Lower Campanian, reappearing in the Lower Campanian *Gonioteuthis quadrata* Zone. It is also present in the Upper Campanian Weybourne Chalk at Keswick, in a single sample of the basal *mucronata* Chalk at Eaton, and in the upper two samples of the Paramoudra Chalk at Whitlingham. The species is also a very rare element in the Lower Maastrichtian pre-*Porosphaera* Beds of Sidestrand. In the Trunch Borehole, it first appears in the Lower Campanian *Gonioteuthis quadrata* Zone (FAD SAG 540) and disappears in the sample immediately above the Campanian - Maastrichtian boundary (basal Lower Maastrichtian, LAD SAG 231).

Asciocythere sp. 2

(not illustrated)

Diagnosis. A more elongate species with a weakly arched dorsal; rounded anterior and posterior margins.

Dimensions.	L	H
SAG 101	0.45	0.31

Depository. Assemblage slides SAG 101, 154.

Material. 5 specimens (outcrop).

Remarks. Left in open nomenclature due to their rarity, specimens of species 2 were separated from species 1 only after SEM photography had been completed. They are, therefore, not illustrated.

Range. This species is restricted to the Upper Campanian Weybourne Chalk (zone/subdivision 12) in the outcrop samples. In the Trunch Borehole, it is slightly more common and wider ranging; it first appears in the *Gonioteuthis quadrata* Zone of the Lower Campanian (zone/subdivision 9) and extends up into the Lower Maastrichtian *Porosphaera* Beds (Zone/subdivision 16, LAD SAG 216).

Asciocythere sp. 3

(not illustrated)

Diagnosis. A small elongate species of *Asciocythere* with a weakly rounded dorsal margin and a rather narrow, angular posterior; lateral surface smooth except for a few scattered pits

Dimensions.	L	H
SAG 427	0.45	0.33

Material. Fewer than five specimens

Range in this study. This species is restricted to the Upper Campanian of the Trunch Borehole, extending into the basal Lower Maastrichtian (SAG 231, pre- *Porosphaera* Beds). It first appears in SAG 427, in the basal *mucronata* Chalk, the second sample above the Lower Campanian - Upper Campanian boundary.

Asciocythere sp.4

(not illustrated)

Dimensions.	L	H
SAG 102	0.41	0.29

Depository. Assemblage slide SAG 102.

Material. 1 specimen.

Range in this study. This rare species, left in open nomenclature and without illustration due to its extreme rarity and fragmentary nature of the specimen, was found in a single sample from the Upper Campanian Weybourne Chalk at Keswick. It has possibly been reworked.

Family EUCYTHERIDAE Puri, 1954.

Genus EUCYTHERE Brady, 1868.

Treatise reference: Q 285

Treatise diagnosis. " Carapace shaped like that of *Cytheridea* except somewhat more triangular, males more elongate than females. Hinge lophodont, formed of interlocking flanges; marginal areas broad anteriorly where line of concrescence departs from inner margins; radial canals few; muscle scars in oblique row of 4 with large heart shaped or V-shaped scar in front (divided in some Cretaceous species). U. Cret.-Rec."

Remarks. *Eucythere* has a similar outline to some species of *Paracyprideis,* but differs in the structure of the maginal zone and hinge structure. Van Morkhoven (1963, p. 240) discusses the use of *Rotundracythere* to accommodate *Eucythere* species with a crenulate median element. The former is used in deep-sea faunas as a separate genus, since modern *Eucythere* species have lophodont hinges in which all the elements are smooth.

After discussion with Professor R. C. Whatley (pers. comm. October, 1999, January, 2000), *Eucythere* will be placed in the Eucytheridae, following the forthcoming *Treatise* revision, currently in preparation. Figure 2.1 (p. 156) illustrates the revised grouping for the Cytherideidae and Eucytheridae:

Eucythere ovoides sp. nov.

Pl. 9, figs 12-17

Derivatio nominis: L. with reference to the imperfect ovoid shape of this species.

Holotype. Female LV (MPK 11469)

Type level. SAG 112, Upper Campanian Paramoudra Chalk

Type locality. Thorpe, Norfolk

Diagnosis. Typically eucytherine in shape, but can be differentiated from other Cretaceous species by its larger size, the broadly rounded anterior margin, narrowly rounded posterior, arched dorsal margin and strong sexual dimorphism. It also appears more inflated than many other representatives of the genus.

Description. Medium, rather heavily calcified. Triangular in lateral view. Anterior margin smooth and broadly rounded; apex at mid-height; dorsal margin broadly rounded, apex at approximately two-thirds length, sloping to a rounded posterior, apex at mid-height. Ventral margin smooth and relatively short, straight to slightly convex. Lateral surface smooth. Sexual dimorphism very pronounced; males more elongate and narrower than females; females more inflated with more broadly rounded anterior and posterior margins. LV > RV. Juveniles distinguishable from adults by smaller size, narrower marginal zone and simple hinge structure.

Inner lamella wide anteriorly, narrow in ventral and posterior regions; avestibulate; marginal pore canals few, straight, simple, widely spaced and often indistinct. A few large marginal pores were seen in a single RV specimen. Muscle scars indistinct or partially obscured. Hinge modified lophodont, not clearly seen. However, in RV, the terminal elements are positive structures separated by a smooth groove that is retained by what seems to be a dentate anti-slip bar.

Dimensions.	L	H
Holotype, female LV (MPK 11469)	0.65	0.40
Paratype, male LV (MPK 11467)	0.69	0.36
Paratype, female RV (MPK 11470)	0.61	0.40
Paratype, male RV (MPK 11472)	0.68	0.35

Material. 11 specimens

Remarks. The species differs from *E. sphenarion* sp. nov. in its slightly larger size, more pronounced sexual dimorphism and less elongate, more rounded posterior. The anterior margin is also more broadly rounded and the carapace more heavily calcified.

Range in this study. Restricted to the uppermost Upper Campanian - Paramoudra Chalk to the Lower Maastrichtian *Ostrea lunata* Chalk and Grey Beds of Trimingham.

Eucythere sphenarion sp. nov.

Pl. 9, figs 6-11

Derivatio nominis: Gr. σφηναριον sphenarion - a wedge, with reference to the shape in lateral view.

Holotype. Female RV (MPK 11464)

Type level. Upper Campanian Beeston Chalk.

Type locality. Caistor St Edmund, Norfolk.

Diagnosis. Typically eucytherine in shape; closely resembles other published Cretaceous species from which it is differentiated by its size, broadly rounded anterior margin, nearly straight ventral margin and the angle by which the dorsal margin, broadly rounded until about mid-length, slopes down to the narrowly rounded posterior.

Description. Medium. Rather thin-shelled. Triangular in lateral view; anterior margin smooth and broadly rounded, apex at mid-height; dorsal margin broadly rounded, apex at approximately two-thirds length, sloping to a narrowly rounded posterior; apex at mid-height. Ventral margin smooth and relatively short, with a slight concavity at about mid-length in RV; ventral margin in LV straight. Lateral surface smooth; ocular tubercle and internal ocular sinus absent. Sexually dimorphic, males more elongate and narrower than females. LV > RV. Juveniles distinguishable from adults by their narrow marginal zone and simple hinge structure; partial ontogeny seen with the smallest instars averaging 0.46mm in length and the largest (A1?) ranging from 0.55 to 0.58mm. Inner lamella wide anteriorly, narrow ventrally and posteriorly; avestibulate; marginal pore canals few, straight, simple, widely spaced and often indistinct. Muscle scars indistinct or partially obscured, consisting of an arcuate row of four adductor scars; frontal scar not seen. Hinge modified lophodont as in *Eucythere ovoides* sp. nov.

Dimensions.	L	H
Holotype, female RV (MPK 11464)	0.62	0.33
Paratype, male LV (MPK 11462)	0.64	0.35
Paratype, female RV (MPK 11463)	0.61	0.33
Paratype, male LV (MPK 11465)	0.62	0.33
Paratype A-1 juv. RV (MPK 11466)	0.58	0.30

Material. 20 specimens.

Remarks. The species is similar in shape and outline to *Eucythere solitaria* Triebel, 1940 (see also Neale, 1978, pl. 1, fig. 11, specimens from the Middle Albian, Speeton Clay), but is much larger, with only juveniles being the same size as Triebel's material. *Eucythere trigonalis* Jones & Hinde, 1890 (Neale, 1978, pl. 1, fig. 10; Wilkinson, 1988b. pl. 3, fig. 7) differs in its more rounded anetrior and dorsal margins; the dorsal margin is nearly convex, sloping down to a very narrow posterior. It differs from *Eucythere ovoides* sp. nov., in its smaller size, less pronounced sexual dimorphism and a more elongate posterior. In the latter species, the anterior margin is also more broadly rounded, the posterior is broader and elongate and the shell more heavily calcified.

Brouwers & Hazel, 1978, describe *E. alexanderi* from the Upper Cretaceous of Alabama and Arkansas. The holotype is Maastrichtian and differs from the present species in its smaller size; it is also more elongate and less strongly arched dorsally. Weaver, 1982 (pl. 6, figs 3-5) assigned a new species

P. cuneiformis to the genus *Phodeucythere* Gründel, 1978, which, in Weaver's opinion is conspecific with *Eucythere* sp. 1 Colin, 1974. This species is very similar to the present species but is less posteriorly elongate and narrower in the anterior marginal area.

Range in this study. In the Trunch borehole, the species has a short range and is a relatively rare component in the samples in which it occurs; First appearance SAG 417, Last appearance SAG 336. It is restricted to the Upper Campanian Beeston and Weybourne chalks.

In the outcrop samples, the range is Upper Campanian to Lower Maastrichtian, but the species is more abundant in the Upper Campanian. It is, however, a rare component throughout the assemblages of the present study.

Table 2.1 (p. 157) compares and contrasts the two taxa; the present author considers *Phodeucythere* to be a junior synonym of *Eucythere* Brady, 1868, which predates it by over a century.

Eucythere sp. 1

Pl. 9, figs 18, 19.

Diagnosis. A rather large species of *Eucythere* with a very broadly rounded anterior margin and a narrow posterior; dorsal margin short and straight.

Dimensions.	L	H
LV (MPK 11473)	0.74	0.41
RV (MPK 11474)	0.75	0.43

Depository. MPK 11473 - 11474

Material. 4 specimens.

Remarks. This species, possibly new but left in open nomenclature due to its sparce record, is larger and more broadly rounded than either *E. ovoides* or *E. sphenarion*. It differs in shape from other Cretaceous published species of this genus and is significantly larger than *Eucythere solitaria* or *E. trigonalis*. It is also broader and appears more inflated.

Figure 2. 1. Revised groupings of the Cytherideidae

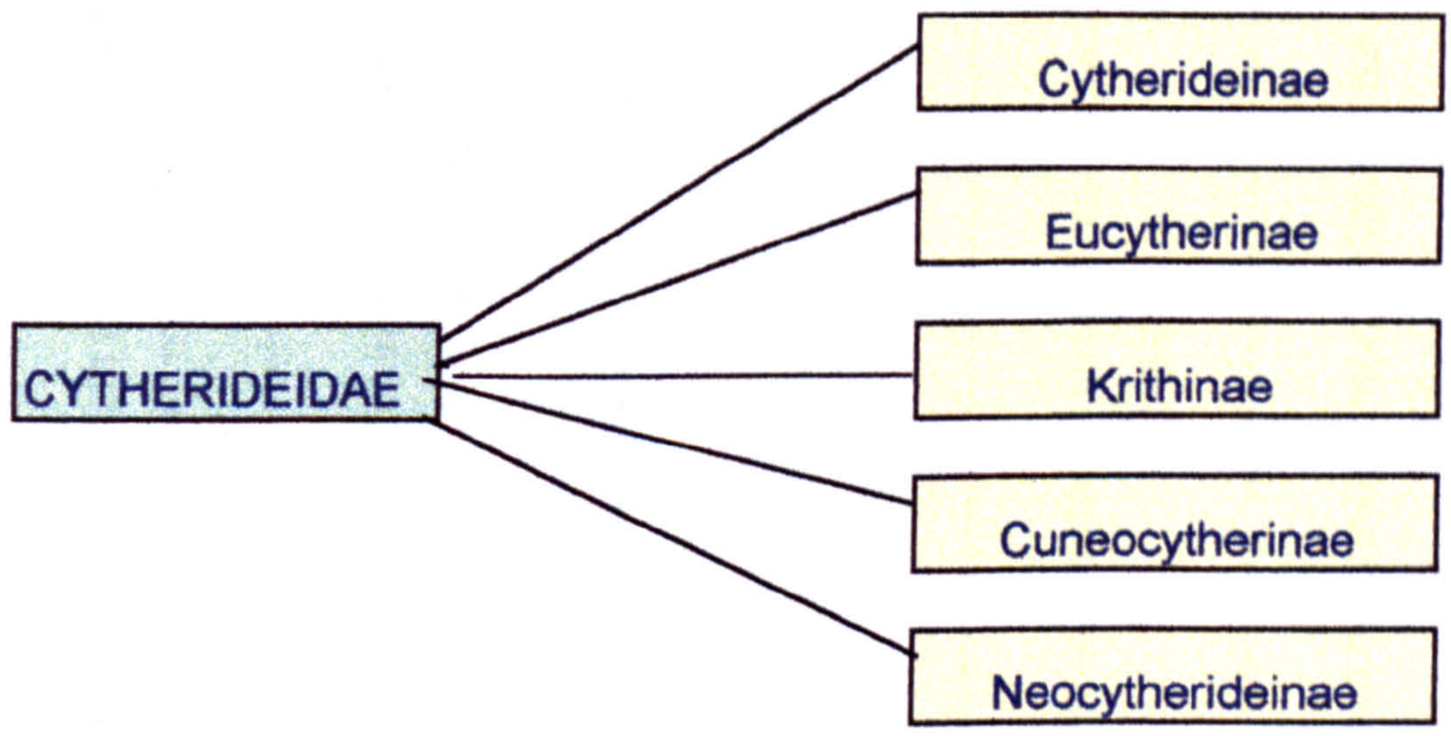


Table 2.1 - Characteristics of *Eucythere* Brady, 1868, and *Phodeucythere* Grundel, 1978

	Eucythere	***Phodeucythere***
shape	Triangular, anterior margin broadly rounded; posterior margin narrowly rounded, elongate	Triangular, anterior margin broadly rounded; posterior margin narrowly rounded, elongate
hinge structure	Lophodont - merodont; terminal elements weakly crenulate, median groove smooth bar, corresponding weak, smooth ridge	Lophodont; LV weak, smooth median bar; RV corresponding weak groove
marginal zone	Broad anteriorly where line of concrecence departs from inner margins, narrower at posterior; few radial canals; usually avestibulate	Broad marginal zone; crescentic vestibule at anterior
muscle scars	Oblique row of four with large heart shaped or V-shaped frontal scar	vertical row of 4 anterior scas, frontal scars not seen by Weaver.
type species	*Cythere declivis* Norman, 1865; by subsequent designation Brady & Norman1889	*Pontocypris trigonalis* Jones & Hinde, 1890, by original diagnosis

Family CYTHERURIDAE Müller, 1894
Subfamily CYTHERURINAE

Genus EUCYTHERURA Müller,1894.

Treatise reference. Q293

Treatise diagnosis. "Carapace small, sub-rhombic to quadrate in side view, inflated, thin walled; anterior margin broadly rounded; posterior margin with caudal process in dorsal half. Surface tuberculate or reticulate; eye tubercle present. Range Cretaceous – Recent."

Weaver, 1982 (p. 86). "Inner lamella moderately wide, avestibulate. Hinge merodont with smooth terminal teeth and smooth to crenulate median groove in RV."

Eucytherura dorsotuberculata Van Veen, 1938
Pl. 9, figs 20-23; Pl. 10, figs 2-5.

1936 "no. 8" Van Veen, p. 179, pl. 10, figs 55-57.

1938 *Eucytherura dorsotuberculata* Van Veen, p. 17.

1941 *Eucytherura dorsotuberculata* Van Veen. Bonnema, pl. 5, figs 45-46.

1949 *Eucytherura dorsotuberculata* Van Veen. Weingeist, p. 367, 369, 371.

1958 *Eucytherura dorsotuberculata* Van Veen. Howe & Laurencich, p. 335-336.

1964 *Eucytherura (Vesticytherura) multituberculata* Van Veen. Gründel, p. 748, pl. 2, figs 12-13.

1965 *Eucytherura (Vesticytherura) multituberculata* Van Veen. Herrig, p. 876, pl. 29, fig. 4a-c.

1966 *Eucytherura (Vesticytherura) multituberculata* Van Veen. Gründel, p. 42, pl. 7, figs 28-29.

1966 *Eucytherura (Vesticytherura)* sp. Gründel, pl. 7, fig. 40.

1982 *Eucytherura dorsotuberculata* Van Veen. Weaver, pl. 16, figs 21-23.

Diagnosis. A small and distinctive species of *Eucytherura*; dorsal and ventral margins straight, anterior margin rounded. Lateral surface with a row of four rounded tubercles; posterior tubercle is slightly elongate, separate from the other three. Eye tubercle large, prominent. A ventro-lateral rib extends from the eye across the antero-ventral surface.

Dimensions.	L	H
LV (MPK 11477)	0.40	0.14
RV (MPK 11476)	0.38	0.12

Depository. MPK 11475-11482.

Material. Over 100 specimens.

Remarks. Gründel's *Eucytherura* sp. is, from the illustrated specimen, synonymous with *E. dorsotuberculata*, but at 0.35mm in length, the former is smaller than the material of the present study. *E. multituberculata* is also considered to be conspecific (junior synonym). Some workers (e.g. Gründel, 1964) divide the genus into subgenera *Eucytherura* and *Vesticytherura* on the basis of the presence or absence of anterior vestibulae. The present author agrees with Symmonds (MS, 1996) in that separating the two is impractical due to the small size and opaque nature of the valves.

The material of the present study is very similar to specimens figured from the Campanian to Maastrichtian of the Maastricht area (Robaszynski *et al.*, 1985). *Eucytherura ansata* Weingeist, described by Kaye (1964, pl. 4, figs 1-4) from the Middle Albian of the Speeton Clay, differs from *Eucytherura dorsotuberculata* only by the spacing of its dorsal tubercles.

Stratigraphical range and distribution. Upper Campanian to Maastrichtian of the Maastricht area and in the British Chalk; Upper Maastrichtian, South Limburg, Belgium, Northeast Holland (Robaszynski *et al.*, 1985, Herrig, 1965).

Range in this study. In the Trunch Borehole, this species first appears in a single Santonian sample from the upper part of the *Marsupites testudinarius* Zone (FAD SAG 637) but is absent in the Lower Campanian *pilula* Zone (7) and the lower part of the *Gonioteuthis quadrata* Zone (9), reappearing in SAG 488. It is more abundant in the Upper Campanian assemblages and extends into the *B. lanceolata* Zone (Lower Maastrichtian, LAD SAG 216). In the outcrop assemblages, it ranges from the Coniacian to Lower Maastrichtian; it first appears in the Coniacian basal *coranguinum* Zone and also in the two upper zones of the Coniacian. It disappears at the Coniacian to Santonian boundary and is absent in the Santonian and lower levels of the Lower Campanian. It reappears in the restricted *quadrata* Zone of the Lower Campanian and is present in the Upper Campanian basal *mucronata* Chalk and in all the other zones/subdivisions of the Upper Campanian. It also occurs in the Lower Maastrichtian *O. lunata* Beds and Grey Beds of Trimingham and pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand.

Eucytherura tumida Bonnema, 1941.

Pl. 10, figs 6-10.

1941 *Eucytherura tumida* Bonnema, p. 23, pl. 5, figs 69-77.

1958 *Eucytherura tumida* Bonnema. Howe & Laurencich, p. 341.

Diagnosis. A small, subquadrate and strongly reticulate species of *Eucytherura*. Dorsal margin straight, ventral margin parallel, weakly convex, anterior margin gently rounded.

Dimensions.	L	H
LV (MPK 11484)	0.45	0.23
LV (MPK 11485)	0.46	0.25
RV (MPK 11486)	0.45	0.24
RV (MPK 11487)	0.43	0.24

Depository. MPK 11484-11488

Material. Over 100 specimens.

Remarks. This species exhibits a range of overall morphology and a degree of variation in the reticulate ornamentation. *E. beaussetensis* Babinot, 1970 (pl. 3, fig. 34; Babinot, 1979; Babinot, 1980, pl. 43, figs 14-17; Oertli *et al.*, 1985, pl. 68, fig. 9; Babinot, 1987, pl. 1, fig. 6) is rather similar in ornament, but lacks the prominent rim around the anterior and ventral margins.

Weaver (1982, p. 88, pl. 16, figs 5-7) illustrates *Eucytherura gruendeli,* a new species from the Middle Cenomanian of Hertfordshire. This species is smaller than *E. tumida* and has two muscle nodes. The eye tubercle is also smaller and the fossae are larger and less celate.

Stratigraphical range. Bonnema records the species from the Upper Chalk of the Netherlands.

Range in this study. In the Trunch Borehole, this species first appears in the Lower Campanian *Gonioteuthis quadrata* Zone (FAD SAG 504) and ranges throughout the Upper Campanian (but not in the basal *mucronata* Chalk (zone/subdivision 10), disappearing in the *B. lanceolata* Zone of the Lower Maastrichtian (LAD SAG 216). In the outcrop assemblages, it ranges from the Coniacian to Lower Maastrichtian; it first appears in the higher levels of the *coranguinum* Zone of the Coniacian and occurs both at Litcham and South Pickenham (1.0-3.7% abundance). It is absent in the Santonian and Lower Campanian, reappearing again in the Upper Campanian basal *mucronata* Zone at Cringleford where it reaches a maximum abundance (SAG 107) of 3.3%. It is also present in all other zones and subdivisions of the Upper Campanian and in the Lower Maastrichtian *O. lunata* and Grey Beds of Trimingham and pre-*Porosphaera* Beds of Sidestrand. The species is slightly more abundant at Sidestrand, with a maximum abundance of 4.0% (SAG 2017).

Eucytherura sp. cf. *E. simplex* Van Veen, 1938.

Pl. 10, fig. 1.

cf. 1936 *Cythereis pulchella* (Bosquet). Van Veen, pl. 5, fig. 13.

cf. 1938 *Eucytherura simplex* Van Veen, p. 17.

Diagnosis. A small, sub-quadrate species with a rather pointed posterior. Ornament not reticulate, eye tubercle small.

Dimensions.	L	H
LV (MPK 11483)	0.42	0.21

Depository. MPK 11483 and assemblage slides (SAG 11, 51-52, 55-57, 79-80, 83).

Material.11 specimens.

Remarks. It should be noted that this species appears in the range charts and assemblage data tables (volume 2, chapter 3) under the name *Eucytherura* cf. *E. solitaria.*

Stratigraphical range and distribution. Recorded by Van Veen from the Senonian "Tuffkreide" from South Limburg, Netherlands, in beds underlying the Maastrichtian or basal Maastrichtian "Koprolithenschichten."

Range in this study. Does not appear in the Trunch Borehole; range in the outcrop samples is Upper Campanian to Lower Maastrichtian. It is seen in the Upper Campanian basal *mucronata* Chalk at Eaton, in samples from Catton Grove, in the Beeston Chalk at Caistor St Edmunds and in the Paramoudra Chalk at Crown Point Pit, Whitlingham. It is slightly more abundant in the Lower Maastrichtian *O. lunata* and Grey Beds of Trimingham.

Eucytherura sp. 1

Pl. 10, figs 11-12.

Diagnosis. This is a heavily calcified species of *Eucytherura*; sub-quadrate with a very large, hemispherical eye tubercle and deep celate reticulation.

Dimensions	L	H
RV (MPK 11489)	0.45	0.26

Depository. MPK 11489, 11490, and various assemblage slides.

Material. 12 specimens.

Remarks. This species is distinguished from other *Eucytherura* in the present study by its celate, almost trefoil shaped, reticulation. In size and shape, it is very similar to *Eucytherura tumida.*

Range in this study. Coniacian -?- Upper Campanian – Lower Maastrichtian. The species is first seen in the higher *coranguinum* Zone at Litcham and South Pickenham, but is absent in the Santonian and Lower Campanian. It appears again in the Upper Campanian basal *mucronata* Chalk at Cringleford and in the Upper Campanian at Stoke Holy Cross. It is also present in the Beeston Chalk at Caistor St Edmunds and in the upper levels of the Paramoudra Chalk at Crown Point Pit, Whitlingham. The species also occurs in the Lower Maastrichtian, sporadically in the *O. lunata* Chalk at Trimingham. It is, however, more abundant in the Upper Campanian and was not seen in the Grey Beds at Trimingham or in the *Porosphaera* or pre-*Porosphaera* Beds of Sidestrand.

Eucytherura sp. 2

(not illustrated)

Diagnosis. A small, rather elongate species with a clear eye tubercle and reticulate ornament.

Dimensions.	L	H
LV (SAG 80)	0.40	0.21

Depository. Assemblage slides SAG 80 and 58.

Material. 2 specimens.

Remarks. Like *E. dorsotuberculata* in shape but lacks tubercles; differs in its weak reticulate ornament.

Range in this study. This species is restricted to the higher horizons of the Upper Campanian outcrop samples. A single specimen was found in the Beeston Chalk at Caistor St Edmunds and a second specimen from the Paramoudra Chalk at Crown Point Pit, Whitlingham.

Family PARACYTHERIDEINAE Puri, 1957.

Genus HEMIPARACYTHERIDEINAE Herrig, 1963.

Diagnosis. (Weaver, 1982, p. 92): "Valves small, sub-rectangular with caudal process in the posterodorsal region; eye tubercle well developed. Valves strongly ornamented, usually with reticulation; hinge of right valve consisting of a strong anterior tooth, crenulated median bar, more strongly developed at anterior."

Remarks. *Hemiparacytheridea,* with its type species *Paracytheridea (Hemiparacytheridea) occulta* Herrig, 1963, is placed by Gründel (1975, p. 657) within the subfamily Paracytherideinae. Gründel's text figure 4 (p. 658) and description, and the work of later authors, shows that *Hemiparacytheridea* is very different to

the genus to which it was originally assigned before Herrig's 1963 paper on new ostracod species (and genera) from the Lower Maastrichtian Schreibkreide of Germany.

Hemiparacytheridea sp. cf. *H. longicauda* (Bonnema, 1941)

Pl. 10, fig. 13.

cf. 1941 *Eucytherura longicauda* Bonnema, p. 24, pl. 5, figs 95-103.

cf. 1966 *Paracytheridea (Hemiparacytheridea) longicauda* (Bonnema). Gründel, pl. 7, figs 20-22.

cf. 1982 *Hemiparacytheridea* cf. *H. longicauda* (Bonnema). Weaver, p. 92, pl. 16, figs 18-20.

Diagnosis. A small, relatively heavily calcified and inflated species; sub-quadrate; dorsal margin straight, posterior margin elongated and drawn out, anterior margin obliquely rounded; eye tubercle large. Ornament strongly reticulate, muri slightly spinose.

Dimensions.	L	H
(MPK 11491)	0.37	0.19

Depository, MPK 11491

Material. 3 specimens

Remarks. The present material is similar to Bonnema's 1941 specimens. Some of the specimens illustrated by Herrig (1966) from the White Lower Maastrichtian Schreibkreide of Germany show a well-defined muscle node, which is not well defined in Weaver's cf. *H. longicauda* from the British Cenomanian. The present material is closer to that of Weaver and Herrig's specimens are, therefore, omitted from the synonymy.

Stratigraphical range and distribution. Bonnema recorded the species from the Chalk of the Netherlands; Weaver (1982) recorded *H. cf. H. longicauda* from various localities in the Lower Cenomanian (Cambridgeshire, Hertfordshire, Kent, Sussex, the Isle of Wight, Dorset.)

Range in this study. This species is rare and rather sporadic in its range, occurring in the Upper Campanian samples at Keswick (SAG 101) and in the Lower Maastrichtian Grey Beds of Trimingham (SAG 2010).

Hemiparacytheridea minutissima (Kaye, 1965)

Pl. 10, fig. 14.

1965a *Orthonatacythere minutissima* Kaye, p. 239, pl. 8, figs 5-11.

1973 *Paracytheridea* aff. gr. *occulta* Herrig. Colin, p. 29, pl. 6, fig. 8.

1982 *Hemiparacytheridea minutissima* (Kaye). Weaver, p. 93, pl. 16, figs 15-17.

Diagnosis. A small, heavily reticulate species, in which horizontal muri dominate, with a ventro-lateral rib that becomes alate at posterior; hinge ear small; dorsolateral node large at two-thirds length.

Dimensions.	L	H
(MPK 11492)	0.35	0.17

Material. 3 specimens.

Remarks. The present material is very similar to specimens illustrated by Kaye (1965), Colin (1973) and Weaver (1982). The ornament is a little more strongly reticulate and the slight hinge ear differentiates it from *H. longicauda*; the stratigraphical range is also significantly different.

Kaye placed the species in the genus *Orthonotacythere* Alexander, 1933, considering it atypical of the genus. It does, however, conform closely to *Hemiparacytheridea* as interpreted by Neale, 1973. Colin (1973) illustrates specimens assigned to *Paracytheridea* aff. gr. *occulta* from the French Cenomanian. These are much more like *H. minutissima* and are included in synonymy for this species.

Stratigraphical range and distribution. Kaye (1965) described the species from the Upper Albian of Kent; Colin (1973) records it in the French Upper Cenomanian, while Weaver describes it from various localities from the British Cenomanian.

Range in this study. This species is extremely rare in the present study, possibly due to its small size. It was recovered in the Upper Campanian from one sample of the Weybourne Chalk at Keswick (SAG 101) and one sample of the Paramoudra Chalk at Crown Point Pit, Whitlingham (SAG 79). It was also seen in the Lower Maastrichtian pre-*Porosphaera* Beds at Sidestrand.

Hemiparacytheridea occulta occulta (Herrig, 1963)

Pl. 10, fig. 15.

1963 *Paracytheridea (Hemiparacytheridea) occulta occulta* Herrig, p. 300, pl. 3, figs 5-7.

Diagnosis. A species of *Hemiparacytheridea* with a very large ocular tubercle, a distinct concave upwards postero-dorsal loop and an incline "L-shaped" rib which links the sub-central tubercle and the sub-alar complex which bears a sharp conical spine. Inter-tubercular ornament is micro-punctate.

Dimensions.	L	H
RV (MPK 11493)	0.39	0.18
SAG 2017	0.41	0.18

Depository. MPK 11493, assemblage slides 2006, 2017.

Material. 3 specimens.

Remarks. This distinctive species is distinguished from others of the genus by its ornament. The material of the present study is identical to that figured by Herrig, 1963. *Paracytheridea* aff. gr. *occulta* Colin, 1973, is, in the present study, assigned to *Hemiparacytheridea minutissima* Kaye, 1965.

Published range. Herrig first recorded the species from the Upper Campanian of Germany.

Range in this study. Restricted to the Lower Maastrichtian Grey Beds of Trimingham and the pre-*Porosphaera* Beds of Sidestrand.

Genus PEDICYTHERE Eager, 1965.

Diagnosis. Eager (1965, p. 21, pl. 2, figs 6-8): "Carapace small, roughly quadrate in lateral outline with a posterior caudal process, ventrolateral ala, postero-ventral process and an amphidont hinge. Dorsal margin straight, becoming concave posteriorly; convex ventral margin; anterior margin broadly rounded.

Anterior margin broadly rounded, anterior peripheral area filled with a few weakly developed ribs. Carapace laterally compressed; posterior end with a small, narrow, straight or slightly upturned caudal process. Weak eye spots may be present. A small, quadrate and a fairly large angular process, both posteriorly directed, posterior to a ventro-lateral pointed ala. There is a small median sulcus on the ala. Hinge amphidont, consisting in RV of an anterior tooth, adjacent socket, a crenulated median groove and a posterior tooth".

Generic range. The genus *Pedicythere* was originally described by Eager from the London Clay of Reading. It has since been found in the Upper Cretaceous of the Netherlands and Britain. Viviere (1985, p. 247) discusses the genus and describes four species assigned to *Pedicythere*? from the Cenomanian to basal Coniacian of Northeastern Algeria. Weaver (1982) erected a new species from the Cenomanian of Southern England.

Pedicythere cf. *P. pitstonensis* Weaver, 1982

Pl. 10, figs 16-19

cf 1982 *Pedicythere pitstonensis* Weaver, p. 93, pl. 17, figs 19-21.

Diagnosis. A small and fragile species of *Pedicythere* with strong ventro-lateral ala. Dorsal margin of RV straight with strongly upturned caudal process. Dorsal margin in LV convex. Caudal process in both valves strongly developed; anterior margin asymmetrically rounded; strong ventro-lateral ala. Hinge not well preserved. A small, square anterior tooth and crenulated median groove seen in some specimens.

Dimensions.	L	H
LV (MPK 11194)	0.36	0.18
RV (MPK 11195)	0.41	0.20
RV (MPK 11196)	0.38	0.17

Depository. MPK 11194, 11195, 11196, 11197

Material. 6 specimens.

Remarks. Weaver's illustrated material from the Cenomanian are identical to the material of the present study, from the Lower Campanian to Lower Maastrichtian. The age difference, however, makes it likely that the present material belongs to a closely related new species not previously seen. It is left as cf. *pitstonensis* due to the limited number of specimens. The species itself is very small, fragile and thin-shelled and is easily overlooked; it may also be more susceptible to damage during initial processing. This may account for the sporadic, wide-ranging record in this study, and the rarity of Cretaceous *Pedicythere* species in published studies. Weaver notes that *P. pitstonensis* differs from *Pedicythere trigonoda* (Albian of Germany; Gründel, 1966) by lacking the dorsal rib present in the latter species; the latter also has a straight dorsal margin in both valves. *Pedicythere flutians* of Bonnema, 1941, from the Upper Cretaceous of Holland (refigured by Herrig, 1966) also has a straight dorsal margin in both valves. The caudal process is not as upturned as it is in Weaver's species and the present material. King (MS, 1968) also describes and illustrates *P. flutians* from the British Upper Chalk.

Neale (1975) described *Pedicythere australis* from the Santonian of the Gingin Chalk, Western Australia. This species differs from *P. pitstonensis* and the material of the present study in its straight dorsal margins and shorter, less upturned caudal process.

Viviere (1985, p. 247) describes four species tentatively assigned to *?Pedicythere.* In the opinion of the present author, these are close enough to Eager's original type description to be retained in the genus, but all are significantly larger than the material of the present study or *P. pitstonensis,* as described by Weaver, 1982.

Stratigraphical range and distribution. Weaver (1982, p. 94) first described the species from the Middle Cenomanian of Pitstone, Hertfordshire (type specimens) and from the Lower to Upper Cenomanian of various other localities in Southern England.

Range in this study. In the Trunch Borehole, the species exhibits a sporadic range and is rare and long-ranging. It would be of little use in biostratigraphy because of its rarity. It first appears in the Lower Campanian *Gonioteuthis quadrata* Zone (FAD SAG 462) and disappears in the *B. lanceolata* Zone (Lower Maastrichtian, LAD SAG 216). In the outcrop samples, it is restricted to the Upper Campanian Eaton and Weybourne Chalk; it is seen in two samples (SAG 101, 102) at Keswick and Eaton.

Pedicythere sp. 1

Pl. 10, figs 20, 21.

Diagnosis. A small, rather heavily calcified species with broad anterior margins in both valves. Each valve has a long spine-like ventro-lateral ala arising from a pronounced ventro-lateral rib with a hollow at its base. Each ala has sharp leading and trailing edges and a sharp longitudinal ridge on its vertical surface.

Dimensions.	L	H
LV (MPK 11498)	0.37	0.16
RV (MPK 11499)	0.35	0.15

Depository. MPK 11498, 11499

Material. 8 specimens

Remarks. This species is larger and more heavily calcified than *P. pitstonensis* or *P.* cf. *P. pitstonensis* of this study. It has a broader and more rounded anterior margin, with a narrower ventro-lateral ala. It is probably new but is left in open nomenclature due to the limited number of specimens.

Viviere's *Pedicythere* sp. 4 from the Santonian of Algeria looks rather like *Pedicythere* sp. 1 of this study, in the shape of the dentate anterior margin, dorsal margin and caudal process. It is, however, slightly larger; the ala is much narrower and is straight.

Range in this study. This species has a sporadic range in the outcrop localities, occurring at South Pickenham in the Coniacian low *coranguinum* Zone (SAG 113) and in the lowest sample (Sag 93) of the Upper Campanian Eaton Chalk. This may be, in part, due to its small size. It is, however, more restricted in the Trunch Borehole. It is restricted to the Upper Campanian and first appears in the basal *mucronata* Chalk (SAG 417 FAD), disappearing in the Beeston Chalk (LAD SAG 336).

Pedicythere sp. 2

Pl. 11, figs 1, 2.

Diagnosis. A small species of *Pedicythere* with vertical antero-dorsal and convex antero-ventral margins; an inverted V-shaped rib extending postero-ventrally from the anterior cardinal angle; a short dorsal rib and a pronounced alar spine with sharp leading and trailing edges and a blunt postero-ventral tubercle.

Dimensions.	L	H
LV (MPK 11500)	0.42	0.19
LV (MPK 11501)	0.41	0.19

Depository. MPK 11500, 11501.

Material. 2 specimens.

Remarks. This species is almost certainly new but is left in open nomenclature due to its rarity.

Range in this study. Restricted in the Trunch Borehole to a single sample in the basal *mucronata* Chalk, immediately above the Lower Campanian – Upper Campanian boundary.

Pedicythere sp. 3

Pl. 11, fig. 3.

Diagnosis. A small species of *Pedicythere* with strong ventro-lateral ala. Dorsal margin straight to weakly convex. Caudal process strongly developed; anterior margin asymmetrically rounded and non-dentate.

Dimensions.	L	H
LV (MPK 11502)	0.44	0.21

Depository. MPK 11502

Material. 1 specimen.

Remarks. Like *P.* cf. *P. pitstonensis* in shape but slightly larger. The caudal process is not as strongly upturned and the anterior margin is less dentate.

Range in this study. Restricted to the Paramoudra Chalk (SAG 111) at Tollgate Pit, Thorpe, but not seen in this horizon at Whitlingham.

Pedicythere sp. 4

Pl. 11, fig. 4

Diagnosis. An elongate species of *Pedicythere*, characterised by its strong, backwardly curving ventro-lateral ala; anterior margin broadly rounded with 3 short spines; posterior narrow with one short postero-ventral spine.

Dimensions.	L	H
RV (MPK 11503)	0.47	0.26

Depository. MPK 11503

Material. 1 specimen.

Remarks. This species is probably new, but is left in open nomenclature because of its rarity.

Range in this study. Restricted to a single specimen from the top of the Upper Campanian Beeston Chalk at West Runton (SAG 13), but not seen in this horizon at Caistor St Edmunds.

Genus SEMICYTHERURA Wagner, 1957.

Treatise reference. Q299-300

Treatise diagnosis (but see remarks and revision below):

"Carapace bi-lamellar, fragile, surface smooth or distinctly ornamented. RV slightly larger than LV, overlapping it along dorsal margin, with distinct caudal process. LV hinge with notched elongated anterior pit which is distinctly terminated in front, short bar terminally thickened and crenulated, but with middle smooth. Line of concrescence broad, particularly in posterior. 4 vertical adductors with a group of 3 scars in front, single mandibular scar."

Revision and remarks. The treatise diagnosis is quite inadequate, since it does not mention the single most important characteristic of the genus i.e. the posterior inflexion of the inner margin/line of concrescence. Also, since first described, the range of shape and ornament has been shown to be much greater. A good example of this is the large diversity of *Semicytherura* species described and illustrated by Maybury (1985, MS), where seventy species were seen. A better generic diagnosis is that of Van Morkhoven (1963, p. 346-349) but the genus still needs some revision.

The genus itself is of worldwide distribution. Van Morkhoven (p.346) gives a range of Paleocene to Recent, possibly extending into the Maastrichtian. More recent authors have documented it in the Upper Cretaceous. In the present study, several species are described and illustrated (*Semicytherura fasciculata, Semicytherura* sp. 1, 2, 3); the generic range in the Upper Chalk of Norfolk is Upper Campanian (basal *mucronata* Chalk) to the Lower Maastrichtian Grey Beds.

Semicytherura differs from *Cytherura* in having a wider inner lamella and crenulated hinge element. *Hemicytherura* has a different outline, hinge structure and marginal zone. Van Morkhoven (p. 349) notes that a "detailed study of the rather varied group of species now placed in *Semicytherura* would probably result in subdivision of the genus into subgenera. Specific differences may be very small and consist, for example, of slight but constant variations in the ornamentation and/or small differences in the number and arrangement of the marginal pore canals. Both these feature would seem to be constant within each species."

There is a possibility that the genus *Mayburya* is a subgenus or junior synonym (pers. comm. Prof. R. C. Whatley: October, 1999; January, 2000).

Semicytherura fasciculata sp. nov.

Pl. 11, figs 5-9.

Derivatio nominis: L. *fascis* (diminutive *fasciculus*) a bundle or sheath of rods, with reference to the parallel, numerous longitudinal ribs of this species, with their fanciful reference to the bundle of rods carried by the Roman lectors.

Holotype. Male LV (MPK 11504)

Type level. Upper Campanian Eaton Chalk.
Type locality. Eaton, Norfolk.

Diagnosis. A small, elongate, sub-ovate to sub-rectangular species with a prominent caudal process. Ornament a series of narrow longitudinal ribs and intercostal punctation; eye tubercle small but clear.

Description. Medium. Elongate, sub-ovate to sub-rectangular with a clear caudal process at mid-height. Anterior margin rounded, apex at approximately mid-height; dorsal margin straight; eye tubercle small but distinct, hemispherical. Posterior margin with caudal process. Greatest height at approximately two-thirds length; posterior in males slightly inflated, ventral margin straight, parallel to dorsal margin. Lateral surface ornate, consisting of 8-9 narrow longitudinal ribs extending across the entire length of the valve, separated by intercostal puncta, which impart an overall reticulate appearance. Sexual dimorphism pronounced; male carapaces wider posteriorly and more posteriorly inflated than females. LV slightly larger than RV but RV predominate.

Inner lamella wide anteriorly; avestibulate; marginal pore canals not seen; muscle scars obscured. Hinge modified antimerodont, weakly developed. LV with weakly loculate terminal sockets separated by a denticulate bar.

Dimensions.	L	H
Holotype, male LV (MPK 11504)	0.49	0.35
Paratype, male RV (MPK 11505)	0.48	0.35
Paratype, female RV (MPK 11506)	0.45	0.32
Paratype, female LV (MPK 11507)	0.46	0.33
Paratype, female RV (MPK 11508)	0.45	0.32

Material. 25 specimens.

Remarks. This species does not closely resemble any of the many published species of this genus.

Range in this study. The species ranges from the Upper Campanian to Lower Maastrichtian. In the Lower Maastrichtian, it is restricted to the Grey Beds. It is more abundant in the Upper Campanian.

Semicytherura sp. 1

Pl. 11, figs 10, 11.

Diagnosis. A sub-rectangular, less elongate species of *Semicytherura*. Ornament rather poorly defined, consisting of a series of longitudinal ridges separated by intercostal punctation, making the surface look reticulate. Caudal process sub-dorsal.

Dimensions.	L	H
LV (MPK 11509)	0.48	0.33

Depository. MPK 11509, 11510.

Material. 6 specimens.

Remarks. This species is more sub-rectangular in shape and less elongate than *Semicytherura fasciculata*. The ornament is similar, but less well defined. It is possibly new but was left in open nomenclature due to a paucity of specimens available for study.

Range in this study. The species is restricted to the Upper Campanian. It is present in the upper samples of the Upper Campanian basal *mucronata* Chalk, Eaton Chalk and one sample (SAG 151) at Eaton. It was present at Keswick and in the Paramoudra Chalk at Crown Point and Church Pit, Whitlingham.

Semicytherura sp. 2.

Pl. 11, figs 12-13.

Diagnosis. A species of *Semicytherura* with numerous longitudinal ribs and fine intercostal pits. Eye tubercle is small but distinct; posterior narrow.

Dimensions.	L	H
RV (MPK 11511)	0.46	0.33

Depository. MPK 11511, 11512.

Material. 2 specimens.

Remarks. This species is new, but is left in open nomenclature due to its very sparse record. It differs from *Semicytherura fasciculata* and *S.* sp. 1, most particularly in its ornament. All three species show longitudinal ribbing, but sp. 2 differs in the ornament of the intercostal region. In *S. fasciculata* and *S.* sp. 1, this consists of reticulate puncta, but in species 2, there are only numerous fine, regularly spaced pits. The posterior region was broken in the illustrated specimen and so the nature of the caudal process cannot be compared with other forms present in the material of this study.

Range in this study. This species was found only in the Upper Campanian Paramoudra Chalk (SAG 83) from Church Pit, Whitlingham.

Semicytherura sp. 3.

Pl. 11, figs 14, 15.

Diagnosis. A small to medium sized sub-ovate to sub-rectangular species which differs from all other species in this study in shape and ornament. Eye tubercle small and less distinct; anterior margin rounded, dorsal and ventral margins straight and parallel. Posterior margin ends in a short, sub-dorsally situated caudal process. Ornament consisting of a single longitudinal rib; other ribs significantly reduced or absent, series of regularly spaced punctae anteriorly, posterior ornament becoming more reticulate.

Dimensions.	L	H
LV male (MPK 11513)	0.44	0.29

Depository. MPK 11513, 11514.

Material. 2 specimens.

Remarks. The measured specimen has a clear postero-dorsal tumidity and is, therefore, male. It is new, but is left in open nomenclature due to its rarity. It differs from other species in this genus in its narrower anterior margin which has a faint antero-dorsal rib extending from the eye tubercle, which is smaller and less distinct than *S. fasciculata* or species 1 and 2. The ornament is also different. Most of the longitudinal ribs are absent or reduced. A single longitudinal rib in the middle of the valve is short and does not extend across the entire length of the valve. The posterior inflation is more pronounced than in male specimens of *S. fasciculata*. The caudal process, which in *S. fasciculata* usually occupies a sub-central position, is

more like that seen in species 2 (subdorsal) but the caudal process in species 3 is more pronounced and slightly longer. The dorsal edge is straight but in species 2, it appears slightly concave.

Range in this study. The species is extremely rare and occurs only in Upper Campanian samples from the Beeston Chalk of the Trunch Borehole.

Genus TETRACYTHERURA Ruggieri, 1952.

Diagnosis. (Van Morkhoven, 1963, p. 367) "Subtrapezoidal in lateral outline. Anterior end broadly rounded; posterior end obliquely truncated above, obtusely pointed subventrally. Dorsal margin with more or less pronounced posterior cardinal angle. Ventral margin straight or somewhat sinuate anteriorly, caudal process absent. Generally small (type species 0.38 to 0.43 mm, but some species reach a length of 0.55 mm)."

? Tetracytherura sp.

Pl. 11, fig. 16.

Diagnosis. A small species, sub-trapezoidal in lateral outline; dorsal process with strong posterior cardinal angle, ventral margin straight; lateral surface smooth to very finely punctate.

Dimensions.	L	H
LV (MPK 11515)	0.38	0.21

Material. A single specimen.

Remarks. The specimen assigned to *Tetracytherura* in the present study conforms to the size and shape of the type species but differs in its ornament. It is smooth to very finely punctate, whereas the ornament in the generic diagnosis is described as consisting of "irregular reticulation, formed by low costae carrying numerous small punctae. Intercostal areas punctate.

Range in this study. This species is extremely rare and restricted to a single specimen from the Lower Maastrichtian *Ostrea lunata* Chalk at Trimingham (SAG 2004)

Subfamily CYTHEROPTERINAE Hanai, 1957

Genus CYTHEROPTERON Sars, 1866.

Treatise reference. Q 292

Treatise diagnosis. "Carapace bi-lamellar, in lateral view roughly ovoid, with oblique caudal process that points obliquely upwards (commonly drawn out strongly) and pointed ventro-lateral wing-like processes, which may be feebly developed; RV slightly larger than LV, overlapping it distinctly along hinge length; from presence of narrow vestibule in front middle" (?) "RV hinge with terminal notched tooth plates united by crenulated furrow; marginal pore canals few. 4 subvertically arranged, elongated adductor muscle scars with V-shaped scar in front of dorsal end of adductor row, and small round scar inside V. Sexual dimorphism present but not pronounced. *U. Jur. – Rec.*"

The early taxonomy of this genus is somewhat confused and is summarised in an appendix table.

Cytheropteron cathetos sp. nov.

Pl. 12, figs 10-15.

Derivatio nominis: Gr. καθγτος - poerpendicular, upright, with reference to the strong alae, which would support this species in a vertical position.

Holotype. LV (MPK 11527)

Type level. Upper Campanian Paramoudra Chalk.

Type locality. Crown Point Pit, Whitlingham.

Diagnosis. A small to medium, very strongly alate species of *Cytheropteron* with pronounced punctate ornament.

Description. Small to medium (Maastrichtian representatives slightly larger than earlier specimens). Rather thin-shelled. Posterior margin with small, tube-like caudal process with apex above mid-height. Anterior margin somewhat medianly truncated. Dorsal margin strongly arched, especially in RV, apex at about mid-length. Alae strong, well developed, backward curving and ending in a sharp, hollow point; leading edge with strong rib and depression at base of the process. Ornament of numerous small, well spaced rounded puncta, not visible in poorly preserved specimens. Internal features as for genus.

Dimensions.	L	H
Holotype, LV (MPK 11527)	0.44	0.26
Paratype, LV (MPK 11528)	0.44	0.27
Paratype, RV (MPK 11529)	0.49	0.29
Paratype, LV (MPK 11530)	0.46	0.27

Material. 24 specimens.

Remarks. *Cytheropteron nanissum* Damotte & Grosdidier (1963, pl. 1, fig. 2a-f) is smaller than the present species. Both have rounded anterior margins and are acutely pointed posteriorly but, in the former, the anterior margin is higher and more convex; also in *C. nanissum*, the alae are longer, more antero-ventral in position and backwardly curved. *Cytheropteron pitstonensis* Weaver, 1982, differs in size (smaller), dorsal margin (nearly straight), less pointed posterior and smaller, less pointed alae. *C. harrisi* Skinner, 1956 (of Benson & Tatro, 1964, pl. 3, figs 5, 6) from the Campanian Marlbrook Marl of Arkansas, USA, is similar in size but has a pointed posterior and a bluntly rounded anterior, and lacks the puncta that cover the entire lateral surface of the present species; dorsal margin is also less arched, the alae are smaller with a nearly straight upper surface. In the present species, the upper surface of the alae is curved backwards and ends in a point. *Cytheropteron arguta* Kaye, 1965 (as figured by Wilkinson, 1988 MS, pl. 13, figs 14-15, from the Albian of Eastern England) differs in size and in the distinct caudal process, the inflated, broad ventro-lateral alae and the coarsely punctate-reticulate ornament; the dorsal and ventral margins are straight and parallel.

Range in this study. Occurs in the Upper Campanian of the Trunch Borehole, the type locality and other outcrop localities and in the Lower Maastrichtian Grey Beds of Trimingham

Cytheropteron sp. 1

Pl. 12, figs 16-17.

Diagnosis. A smooth, strongly alate species of *Cytheropteron* in which the leading edge of the ala is enhanced by two parallel ribs.

Dimensions.	L	H
LV (MPK 11533)	0.41	0.23
LV (MPK 11534)	0.41	0.24

Material. More than 15 specimens.

Remarks. Left in open nomenclature at the present time.

Range in this study. This species was restricted to the Upper Campanian. It occurs in the basal *mucronata* Chalk at Cringleford, in the Weybourne Chalk at Keswick, and in one sample of the Paramoudra Chalk at Whitlingham. It was present in the Beeston Chalk at Caistor St Edmunds and in the basal *mucronata* Chalk at Eaton, but not in the higher zones at the latter locality.

Cytheropteron sp. 2

Pl. 12, fig. 18.

Diagnosis. A smooth, sub-ovate (probably juvenile) species of *Cytheropteron* with a triangular alar process enhanced by a series of poorly defined vertical ribs.

Dimensions.	L	H
RV (MPK 11535)	0.43	0.26

Depository. MPK 11535

Material. 2 specimens.

Remarks. Left in open nomenclature due to its rarity.

Range in this study. Present in one sample from the Paramoudra Chalk of Crown Point Pit, Whitlingham.

Cytheropteron sp. 3

Pl. 13, fig. 1.

Diagnosis. A reticulo-punctate species of *Cytheropteron* with a somewhat subdued alar process in which the leading edge comprises two parallel ribs, with several parallel ribs crossing the ventral margin.

Dimensions.	L	H
RV (MPK 11536)	0.43	0.24

Depository.MPK 11536

Material. 1 specimen.

Range in this study. Present in a sample from the Lower Maastrichtian at Overstrand, Norfolk (SAG 2)

Genus AVERSOVALVA Hornibrook, 1952.

Treatise reference. Q 292 (as synonym of *Cytheropteron;* now accorded separate generic status).

Aversovalva apeorus sp. nov.

Pl. 11, figs 17-21; pl. 12, figs 1-9.

Derivatio nominis: Gr. απεορος apeorus – soaring, hanging in the air, with reference to a fanciful flight performed by a species with such large alae.

Holotype. LV (MPK 11519)

Type level. Upper Campanian Beeston Chalk.

Type locality. Caistor St Edmund, Norfolk.

Diagnosis. A small to medium species of *Aversovalva,* characterised by a strongly arched dorsal margin, rounded anterior and posterior margins. Four to five fine parallel ribs cross the ventral margin and extend onto the antero- and postero-ventral surfaces. Ventral margin completely obscured by large, strongly developed ventro-lateral alae which is reticulate; ornament in form of rounded, regularly spaced puncta.

Description. Small to medium. Rather inflated with a strongly arched, smooth dorsal margin, apex at about mid-height. Anterior and posterior margins smoothly rounded, apices at mid-height. There are two variants, an ornate and a rare smoother form. In the former, 4-5 fine parallel ribs cross the ventral margin, extending onto the antero- and postero-ventral surfaces; these are absent in the inornate form. Ventral margin completely obscured by ventro-lateral ala, well developed with about 6 reticulate fossae, anterior part of ala with a small triangle of finer, regularly spaced puncta in the smoother form, less evident in the ornate form. Ornament usually a series of deep, circular, regularly spaced puncta, rarely smooth or finely punctate. RV slightly larger than LV, overlapping it distinctly along the hinge line, especially clear when complete carapaces are seen in dorsal view. Hinge modified antimerodont and well developed. In the LV, the circular terminal sockets are separated by a denticulate bar. Avestibulate. Marginal zone is of medium width, narrower at posterior. Other internal features not seen.

Dimensions.	L	H
Holotype, LV (MPK 11519)	0.49	0.32
Paratype, C (MPK 11516)	0.50	0.34
Paratype, LV (MPK 11517)	0.48	0.33
Paratype, LV (MPK 11518)	0.49	0.33
Paratype, LV (MPK 11521)	0.47	0.34
Paratype, RV (MPK 11524)	0.51	0.35
Paratype, RV (MPK 11526)	0.53	0.35

Depository. MPK 11516-11526.

Material. More than 65 specimens.

Remarks. The majority of specimens are ornate but some from the Santonian and Lower Campanian (e.g. Trunch Borehole SAG 484; Lower Campanian *G. quadrata* Zone) lack the rows of punctae.

Aversovalva arrectihypa Crane, 1965 (p. 204, pl. 3, fig. 4) from the Upper Cretaceous of the USA is similar to the present material in shape and size but differs in the "closely spaced vertical rows of reticulations in the median area of the valve". *A. puncta* Crane, 1965, differs from the previously mentioned species in its vertically orientated rows of reticulations on the mid-portion of its lateral surface,

rather than a punctate surface with puncta arranged in vertical rows. It differs from the present species in its smaller size, less pronounced ventro-lateral alae and punctate ornament, which like *A. apeorus* are arranged in vertical rows, but are much less pronounced. *Cytheropteron nanissum* Damotte & Grosdidier, 1963 (pl. 1, fig 2a-f) from the French Upper Albian, is similar in size but is slightly more elongate with a rounded anterior and slightly pointed posterior. It also has a short rib just beneath the dorsal margin, from which a vertical rib extends down to the alar process. The ornament is smoother. The present material is similar to *Aversovalva v-scriptum* (Van Veen, 1932), illustrated by Damotte, 1971a, pl. 8, fig. 15). However, the ala is less pronounced and non-reticulate; it is also smaller. The puncta are larger and less regularly spaced. In the present species, they are arranged in clear vertical rows; in Veen's species, the V-shaped median furrow is more prominent. The present species differs from *A. tenuiculum* Damotte, 1965 (pl. 1, figs 4a-c) from the French Lower Campanian in its larger size and more strongly arched dorsal margin, larger, backwardly curving reticulate alae and punctate ornament.

Range in this study. In the outcrop samples, the species first appears in the higher levels of the Coniacian *coranguinum* Zone and is present in all zones of the Upper Campanian. It appears at Stoke Holy Cross, Catton Grove and Keswick and also in the basal *mucronata* at Cringleford and Eaton, the Eaton and Upper Weybourne chalks at Eaton and in the Beeston Chalk at Caistor St Edmunds and in all samples from the Paramoudra Chalk at Whitlingham. In the Lower Maastrichtian, it occurs in the *O. lunata* Chalk, Grey Beds of Trimingham; pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand. In the Trunch Borehole, it ranges from the Lower Campanian *Gonioteuthis quadrata* Zone to the Lower Maastrichtian.

Subfamily KRITHIDAE

Genus KRITHE Brady, Crosskey & Robertson, 1874.

Treatise reference. Q 288.

Treatise diagnosis. "Carapace oblong with greatest height at or behind mid-length; anterior end usually rounded; posterior obliquely truncate and usually intumed. Moderately to strongly tumid in dorsal view. LV hinge with longitudinal furrow for reception of sharp dorsal edge of RV; muscle scars in vertical row of four adductors, usually with U-shaped antennal scar in front, but this may be divided into 2 or more scars; mandibular scars usually small."

Krithe bonnemai Deroo, 1966

Pl. 13, figs 2-7.

1966 *Krithe bonnemai* Deroo, pl. 11, figs 243 - 245.

Diagnosis. A broad, elongate species of *Krithe*, smooth, trapezoidal in lateral view with a weakly arched dorsal margin; more inflated than other species appearing in this study.

Dimensions.	L	H
LV (MPK 11537)	0.46	0.27
LV (MPK 11538)	0.46	0.27

RV (MPK 11539)	0.47	0.28

Depository. MPK 11537-11542.

Material. At least 20 specimens.

Remarks. This species is similar to *Krithe polita* Damotte, 1965, also found in the Upper Campanian and Lower Maastrichtian of Norfolk (present study). *K. bonnemai*, however, has a longer range and is larger and more inflated. The latter is also seen in the Coniacian low *coranguinum* Zone at South Pickenham. The Coniacian material is restricted to a few specimens, slightly smaller and narrower than Campanian.

Published range. Deroo describes the species from the Upper Campanian of Holland. It is rare in published records.

Range in this study. *Krithe* cf. *bonnemai* is present in the Coniacian low *coranguinum* Zone at South Pickenham. *Krithe bonnemai* ranges from the Upper Campanian – Lower Maastrichtian, in the basal *mucronata* Chalk at Cringleford, the Weybourne Chalk at Keswick; Upper Weybourne Chalk at Eaton. It is present in the Beeston Chalk at Caistor St Edmund and in the Paramoudra Chalk at Whitlingham. In the Lower Maastrichtian, the species occurs in the *O. lunata* and Grey Beds of Trimingham and in the pre-*Porosphaera* Beds of Sidestrand.

Krithe polita Damotte, 1965

Pl. 13, figs 8-10

1965 *Krithe polita* Damotte, pl. 1, fig. 3a-e; pl. 2, fig. 10a-b.

Diagnosis. A medium species, trapezoidal in lateral view; RV < LV; posterior of carapace forming an angle level with ventral margin; strongly dimorphic (males longer and narrower), with a strongly invaginated margin posteriorly in LV.

Dimensions.	L	H
LV (MPK 11543)	0.47	0.29
RV (MPK 11544)	0.45	0.27

Material. At least 60 specimens.

Remarks. *Krithe vanveenae* Deroo, illustrated by Robaszynski *et al.*, 1985, from the Upper Campanian close to the type Maastrichtian, is smaller, less elongate, with a more arched dorsal margin and a less truncate anterior margin.

Stratigraphical range and distribution. Damotte - French Lower Campanian. Babinot *et al.*, 1983, record, but do not illustrate, it in the Campanian of the Paris Basin.

Range in this study. This species ranges in the outcrop samples from the Upper Campanian to Lower Maastrichtian.

Family LOXOCONCHIDAE Sars, 1925

Treatise reference. Q 312

Treatise diagnosis. "Small, usually dimorphous carapaces, which may be nearly smooth but most are finely to coarsely pitted or reticulate; reniform to rectangularly ovate in lateral view with tendency to develop a posterior caudal process in some genera. Hinge typically gongylodont; in some species with anterior left and right dentition appearing as 2 distinct teeth separated by a deep pit but with these teeth normally united above by narrow crescentic ridge that make horseshoe-shaped structure fitting over single tooth in opposite valve; marginal areas broad, tending to develop vestibules at ends; radial canals few, normal canals widely spaced, large and in some genera sieve-like; adductor scars in slightly oblique row of four elongate spots, antennal scars in slightly oblique row of 4 elongate spots, antennal scar U- or C-shaped, mandibular scars 2 oval spots obliquely below and forward. Habitat shallow marine or brackish water. Cret. – Rec."

Remarks. Several new genera have been added to the Loxoconchinidae since the *Treatise*; these include *Sagmatocythere* Athersuch, 1976, and *Phtanoloxoconcha* Wilkinson, 1988 (based on a species originally assigned to ?*Loxoconcha* by Weaver). These new genera introduce a wider variation in ornament and other characters than originally considered. The family has since been split into the Mandelstaminae (Triassic - Recent) and Loxoconchinae (Cenomanian - Recent), representing an extension of the range.

Subfamily LOXOCONCHINIDAE Sars, 1925

Genus SAGMATOCYTHERE Athersuch, 1976.

Diagnosis. "Carapace elongate, quadrate, sharply truncate posterior, ornament strongly reticulate, post-ocular sinus in male. Posterior hinge element strongly lobed and strongly curved; hinge gongylodont."

Sagmatocythere orthros sp. nov.

Pl. 13, figs 11-24; pl. 14, figs 1-2.

Derivatio nominis: Gr. ορθρος orthros – early, with reference to the stratigraphical occurrence of the species, possibly the first record from the Mesozoic.

Holotype. Female LV (MPK 11546).

Type level. Topmost Upper Campanian, Paramoudra Chalk (SAG 79).

Type locality. Crown Point Pit, Whitlingham.

Diagnosis. A small, strongly dimorphic species of *Sagmatocythere*; subquadrate and reticulate; eye tubercle small, hemispherical, distinct. Anterior margin rounded with narrow, smooth marginal rim; posterior narrowly rounded, dorsal margin straight. Ventral margin rounded in females, straight and almost parallel in males, with small, blunt posterior spine

Description. Small, sub-quadrate in lateral view, not heavily calcified. Dorsal margin straight in both valves. LV >RV; anterior margin dentate and broadly rounded; apex at about mid-height, with narrow, non-reticulate marginal rib. Posterior narrowly rounded, acute, apex above mid-height. Highest point sub-central, two-thirds length. Strongly dimorphic; anterior margin more broadly rounded in females, males

narrower, more elongate, females more inflated. Ventral margin in females rounded, straight in males; both sexes with short, blunt, ventro-lateral process. Eye tubercle small, distinct, hemispherical. Ornament regularly reticulate with square to sub-circular fossae covering entire lateral surface except for narrow, smooth anterior and posterior marginal areas, regularly reticulate on anterior and posterior parts of the valve; centrally, regular pattern of ornament coarser, fossae larger, less regularly spaced, varying in shape. Ornament in late-stage juveniles regular across entire lateral surface. Marginal areas broad; hinge gongylodont.

Dimensions.	L	H
Holotype, female LV (MPK 11546)	0.45	0.27
Paratype, female LV (MPK 11547)	0.45	0.27
Paratype, female LV (MPK 11548)	0.45	0.27
Paratype, male LV (MPK 11549)	0.51	0.25
Paratype, male LV (MPK 11550)	0.49	0.24
Paratype, A-1 juv.? LV (MPK 11552)	0.35	0.20
Paratype, A-1 juv.? RV (MPK 11553)	0.37	0.21
Paratype, female RV (MPK 11554)	0.43	0.26
Paratype, female RV (MPK 11555)	0.42	0.25
Paratype, female RV (MPK 11556)	0.43	0.25
Paratype, male LV (MPK 11557)	0.49	0.24

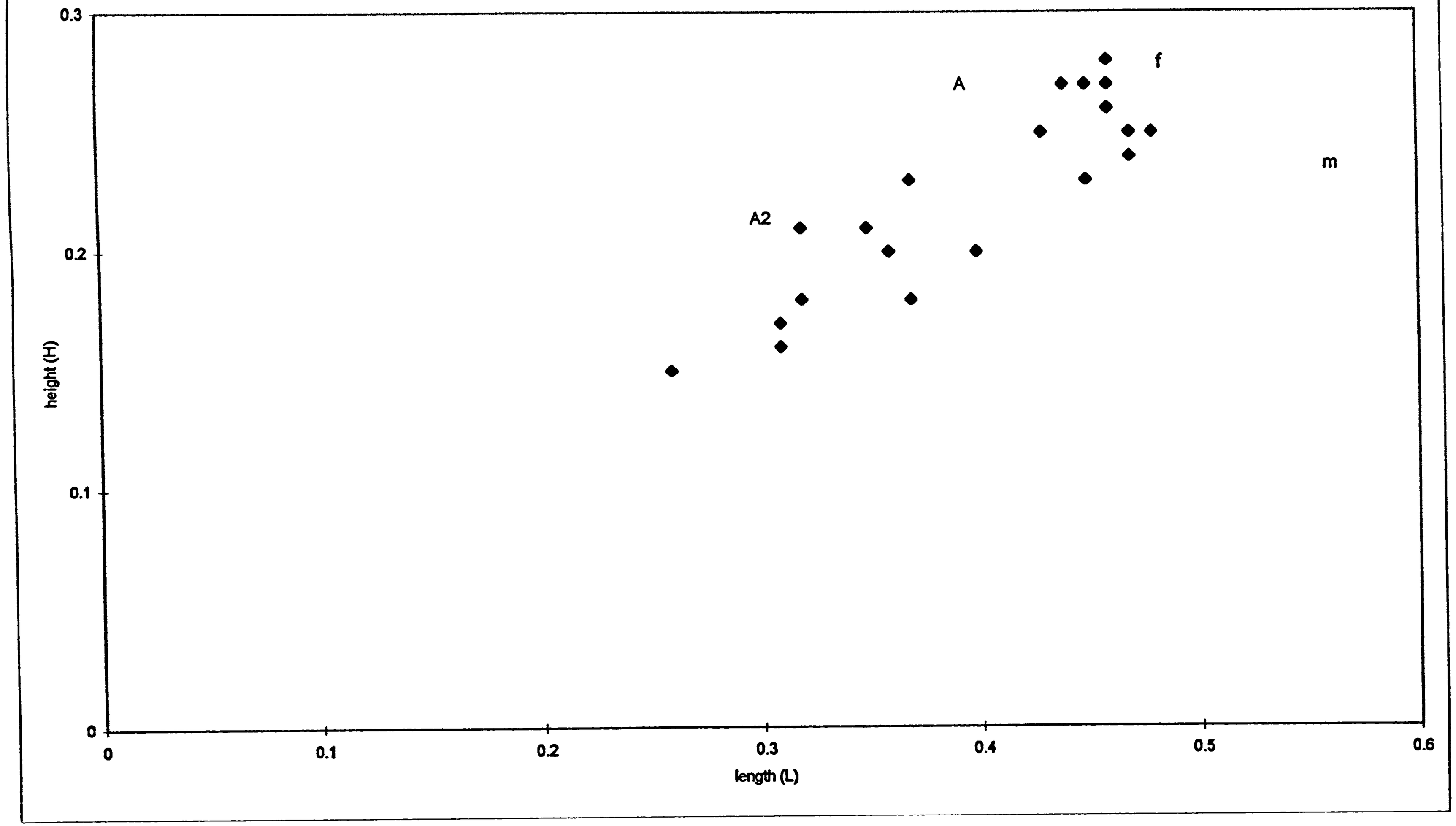
Depository. MPK 11546-11558

Material. More than 40 specimens.

Remarks. The type species, *S. napoliana* (Puri, 1963), retains the basic gongylodont hinge characteristics of *Loxoconcha* but differs in its enlarged, lobed, curved posterior hinge elements, different muscle scar patterns; reticulate ornament, quadrate outline. The genus probably "includes several other species previously considered in *Loxoconcha*." In *S. orthros*, the hinge is similar to the type but the posterior hinge element is not as strongly crenulated. The ornament in the type species is more strongly reticulate with a more open pattern of fossae, the latter is more elongate and the dorsal margin less strongly arched, appearing almost straight. *S. orthros* is similar to *Eucytherura (E.) longisculpta* Weaver, 1982, but differs in size and ornament. The latter differs from others illustrated as *Eucytherura* by Weaver, which all have large sub-central tubercles. It is probable that *E..longisculpta* belongs in the Loxoconchidae. Among the diverse fauna of *Sagmatocythere* described by Maybury (MS., 1985) from the Pliocene of Cornwall and NW France (18 species) are several taxa which closely resemble the present species. The closest in this assemblage is *S. variolata* (Brady, 1878).

Range in this study. In the Trunch Borehole, the range is Upper Campanian to basal Lower Maastrichtian (FAD SAG 417; LAD SAG 231). In the outcrops, the range is similar. It appears in the basal *mucronata* Chalk at Eaton but is absent from higher levels at this locality. It is present in the Upper Weybourne Chalk at Keswick and the upper Beeston Chalk at Caistor St Edmunds. It is ubiquitous and more abundant in the Paramoudra Chalk at Whitlingham. In the Lower Maastrichtian, the species occurs in the *O. lunata* Chalk and Grey Beds of Trimingham and the pre-*Porosphaera* Beds of Sidestrand.

Fig. 2.2. Length - Height diagram drawn for selected specimens of *Sagmatocythere orthros* sp. nov.



Family SCHIZOCYTHERIDAE Howe, 1961.

Genus AMPHICYTHERURA Butler & Jones, 1957.

Treatise reference. Q 331

Treatise diagnosis. "Hinge schizodont, like *Costa*, but smaller, less elongate and with median ridge straight or curved, concave upwards, less well-defined than in *Costa*. Externally, resembles *Eucytherura*."

Revised diagnosis. Size small to medium; sub-rectangular to sub-quadrate in lateral outline. Valves strongly built with three longitudinal ridges on lateral surface, sometimes with reticulation between. Hinge in RV with sub-quadrate crenulate terminal teeth and crenulate median groove, deepened into a rounded socket at the anterior end. This diagnosis follows Weaver, 1982 (p. 97) and other authors, since the 1961 diagnosis is inadequate. The genus *Costa*, for example, has a holamphidont hinge.

Remarks. In outline, *Eucytherura* may resemble *Amphicytherura*, but the latter genus is generally larger with a schizodont hinge; the former genus being antimerodont. Van Morkhoven (1963, p. 360) notes that "in general, in lateral outline *Amphicytherura* resembles *Schizocythere*, which is probably derived from it. In some cases, it is difficult to distinguish between the two genera; more typical species differ in type of ornament and details of hinge structure." This is certainly true in the present study, where species belonging to the two genera are clearly distinguishable.

The genus *Acrocythere* Neale, 1960, is also similar to *Amphicytherura* but differs in its thinner carapace and lack of development of the anteromerodont tooth. Such authors as Bate (1972), Dingle (1982, p. 380) and Symmonds (1996, MS) have included the former genus within the Schizocytheridae. King (MS, 1968, pp 281-286) discusses the relationships of genera placed within this family.

Symmonds (1996, MS, p. 42, 183) notes that there appears to be "a progressive development from an antimerodont hinge through an intermediate stage to the schizodont condition of *Amphicytherura*. The ornamental elements vary in their development but retain the same basic pattern." The same author (MS, p. 32) suggests that species of *Amphicytherura*, a genus of the Schizocytheridae, have evolved from *Acrocythere*. This raises the question of whether the former genus should be placed in the Schizocytheridae to reflect the phylogeny of the group, or left in the Cytheruridae, but this complex issue is beyond the scope of the present thesis and will not be considered further. The phylogenetic lineage proposed by Gründel, 1975 (pp 663-665, text figure 8) are, in the opinion of the present author, greatly oversimplified. Some linkages are made between genera that are disputed by other authors. The links between *Acrocythere* and *Amphicytherura* have, however, been well documented (see also Wilkinson, 1988a, MS, 1988b).

Amphicytherura chelodon (Marsson, 1880)

Pl. 14, figs 3-9.

1880 *Eucythere chelodon* Marsson, p. 43, pl. 3, figs 13a-f.

1890 *Cythereis icenica* Jones & Hinde, pl. 1, figs 37-39.

1958 *Amphicytherura chelodon* (Marsson). Howe & Laurencich, p. 46.

1958 *Amphicytherura icenica* (Jones & Hinde). Howe & Laurencich, p. 48.

1964 *Amphicytherura chelodon* (Marsson). Kaye, pl. 1, figs 6, 7.

1967 *Eucytherura chelodon* (Marsson). Herrig, pl. 1, fig. 12.

1968 *Amphicytherura chelodon* (Marsson). King, MS, Pl. 30, fig. 6-9.

1968 *Amphicytherura icenica* (Jones & Hinde). King, MS, pl. 30, figs 10, 11.

1978 *Amphicytherura chelodon* (Marsson). Neale, pl. 13, figs 11-12.

?1988 *Schizocythere* aff. *chelodon* (Marsson). Robaszynski *et al.*, pl. 21, fig. 6.

Diagnosis. A small, sub-quadrate species of *Amphicytherura* with well developed dorsal, median and ventral ribs; median and dorsal ribs connects; some cross ribbing in anterior areas of valve.

Dimensions.	L	H
Female LV (MPK 11559)	0.47	0.29
Female LV (MPK 11560)	0.50	0.30
Male RV (MPK 11561)	0.46	0.29
Female RV (MPK 11562)	0.45	0.27
Female RV (MPK 11563)	0.44	0.27
Female RV (MPK 11564)	0.44	0.26

Depository. MPK 11559-11564.

Material. Over fifty specimens in the outcrop samples alone.

Remarks. In their 1890 monograph, Jones & Hinde illustrate *Cythereis icenica*, later to be reassigned to the genus *Amphicytherura* by Howe & Laurencich, 1958. The small scale (x 20) of illustration makes identification difficult but later authors include *A. icenica* in synonymy with *A. chelodon*. The present author agrees. King, 1968, (MS, pp 289-291) notes that both species occur in the same samples in Norfolk but considers each as separate forms. The illustrated specimens are, however, almost identical. The present author has included them in synonymy as conspecific with *Amphicytherura chelodon*. The species described by Van Veen (1934) as *Eucytherura chelodon* is not conspecific with *E. chelodon* of Marsson, 1880. It has been identified as *Amphicytherura dubia* Israelsky, 1929. Van Veen also (1938) illustrated specimens of *E. chelodon* which conform to Howe & Laurencich's original description of *A. limburgensis*. Robaszynski *et al.*, 1985, illustrate *Schizocythere* aff. *chelodon*. This is tentatively included in synonymy with the present species, based on the single text figure illustration.

Published range. The species is restricted to the Lower Campanian - Lower Maastrichtian in published records. Neale gives this range for the species in Britain but notes it is slightly more restricted in Norfolk. It was recorded from the Campanian Saratoga Chalk of Arkansas and Texas (Alexander, 1936, p. 692), the Lower Campanian - Lower Maastrichtian of Germany (Herrig, 1967) and the Upper Chalk of Norfolk (Jones & Hinde, 1890; King, 1968 MS; Neale, 1978). It was found in the Chalk of the northeastern Netherlands and the Maastrichtian of Maastricht and South Limburg (Robaszynski *et al.*, 1985).

Range in this study. In the outcrop samples, this species ranges from the Lower Campanian restricted *quadrata* Zone (zone/subdivision 9) to the Lower Maastrichtian. It only appears, however, in one locality in the Lower Campanian (Warham, Norfolk). It is significantly more abundant in the Upper Campanian, where it occurs in a single sample of the basal *mucronata* Chalk (10) at Cringleford, the basal *mucronata* Chalk and Eaton Chalk (11) at Eaton, in all samples of the Weybourne Chalk (12) at Keswick, the upper samples of the Beeston Chalk (13) at Caistor St Edmunds and in most of the Paramoudra Chalk samples

(14) from Whitlingham. In the Lower Maastrichtian, it is present in the pre-*Porosphaera* and *Porosphaera* Beds (15, 16) of Sidestrand, a ubiquitous element in the assemblages of the *O. lunata* Chalk (17) and also occurs in the Grey Beds (18) of Trimingham.

In the Trunch Borehole, *A. chelodon* is restricted to the Upper Campanian. It first appears in the basal *mucronata* Chalk and extends up into the uppermost Paramoudra Chalk (LAD SAG 241).

Amphicytherura falloti Donze, 1972

Pl. 15, figs 4-10.

1972 *Amphicytherura falloti* Donze, p. 384, pl. 2, figs 13-20.

1982 *Amphicytherura* cf. *A. falloti* Donze. Weaver, p. 97, pl. 20, figs 1-3.

Diagnosis. A small, rather heavily calcified species; dorsal margin straight with a small hinge ear in LV; ventral margin straight to weakly convex, parallel to dorsal margin. Anterior margin obliquely rounded; posterior margin pointed with straight lower margin and concave upper margin. Dorsal rib straight and joins large eye tubercle; short oblique rib from eye tubercle parallel to dorsal margin. Median rib strong; ventral rib well-developed, ending in two or three short spines. Three longitudinal ribs on ventral surface of each valve with weak cross ribbing; rest of ornament variably reticulate. Anterior and posterior margins slightly compressed. Hinge schizodont.

Dimensions.	L	H
RV (MPK 11578)	0.40	0.23
LV (MPK 11577)	0.42	0.23
LV (MPK 11580)	0.44	0.25

Material. 12 specimens

Remarks. Weaver assigned his specimens to *A. cf. A. falloti,* but these are included in synonymy with the nominative species, since the present material is shown to be variable in both size and ornament. The differences cited by Weaver (lateral longitudinal ribs less rounded, rib below eye less pronounced; ventral margin more convex) are probably only minor morphological variations. The present material differs in range (Upper Campanian to Lower Maastrichtian, compared to Upper Cenomanian) and shows some morphological variations that are probably attributable to development of this species over time. The eye tubercle in the present material is slightly larger; the ventro-lateral rib is stronger and ends in two to three short spines. The lateral surface is also slightly more reticulate.

Published range. This species has previously been recorded from the Upper Cenomanian of Southern France (Donze, 1972) and various localities in Southern England (Weaver, 1982).

Range in this study. This species was absent from the Trunch Borehole; in the outcrop samples, it was restricted to the Upper Campanian. It is rather sporadic in the basal *mucronata* and Eaton chalks at Eaton (zone/subdivision 10), but not in the higher intervals at that locality. It also occurs in the Beeston Chalk (13) at Caistor St Edmunds and in several samples from the Middle Weybourne Chalk (12) at Keswick. It was present in the Paramoudra Chalk samples (14) at Crown Point Pit and Church Pit, Whitlingham, but does not extend into the Lower Maastrichtian. It is used in the biozonation as a marker

species for the Upper Campanian substage with the erection of an *A. falloti* range Zone, concurrent with the *Monoceratina longispina / Cythereis campaniensis* sp. nov. Range Biozone.

Amphicytherura limburgensis Howe & Laurencich, 1958

Pl. 14, figs 11-22; pl. 15, figs 1-3.

1958 *Amphicytherura limburgensis* Howe & Laurencich, p. 49.

1967 *Amphicytherura limburgensis* Howe & Laurencich. Herrig, pl. 1, text fig. 2.

Diagnosis. A large species of *Amphicytherura*, distinguished by its ornament; a prominent rounded median rib which extends obliquely to the posterior margin; ventral rib connected to anterior margin and obscures straight ventral margin for much of its length. Sub-rectangular in dorsal view, dorsal margin straight. Eye tubercle large and distinct, hemispherical. Anterior margin obliquely rounded; posterior compressed, angled near middle in RV but obliquely truncate in LV.

Dimensions.	L	H
Female LV (MPK 11566)	0.52	0.34
Female LV (MPK 11567)	0.56	0.35
Female RV (MPK 11573)	0.58	0.39
Male RV (MPK 11574)	0.61	0.30
Female LV (MPK 11570)	0.54	0.32

Depository. MPK 11566-11576

Material. Over 50 specimens in the outcrop samples alone.

Remarks. *Amphicytherura dubia* is the type species of this genus (Israelsky, 1929, p. 6, pl. 4A, fig. 6), described from the Campanian of Arkansas (Benson & Tatro, 1964, p. 28, pl. 6, figs 1-3) and by Deroo, 1966 (pl. 20, figs 563-565) from the Upper Campanian to Lower Maastrichtian of Belgium. This is similar to *A, limburgensis* but can be distinguished by its smaller size, straight dorsal margin and lateral compression. *A. berbuigierensis* Colin, 1974 (pl. 10, figs 11-13) from the Upper Cenomanian of Southern France differs in its ornament, with only a median rib.

Published range. Maastrichtian in published records; South Limburg (Howe & Laurencich). Herrig (1967) documents it from the uppermost Lower Maastrichtian of Northeastern Germany.

Range in this study. Much more extensive than the published range. In this study, the range is Lower Campanian -?- Upper Campanian to Lower Maastrichtian.

In the Trunch Borehole, the species first appears in the Lower Campanian *O. pilula* Zone and disappears in the Lower Maastrichtian pre-*Porosphaera* Beds (LAD SAG 221). In the outcrop assemblages, it first appears in the *O. pilula* Zone (zone/subdivision 7) of the Lower Campanian at Wells, Norfolk but is absent at all other localities and from the restricted *quadrata* Zone (9). It is significantly more abundant in the Upper Campanian, where it is present in the basal *mucronata* Chalk (10) at Eaton and Cringleford and the Middle Weybourne Chalk (12) at Keswick. It occurs sporadically in the Beeston Chalk (13) at Caistor St Edmunds and is slightly more common in the Paramoudra Chalk (14) at Whitlingham.

In the Lower Maastrichtian, it is present in the pre-*Porosphaera* Beds (15) at Sidestrand and in the *O. lunata* Chalk and Grey Beds (17, 18) at Trimingham. It reaches a maximum abundance of 4.6% in SAG 2002 (*O. lunata* Chalk)

Amphicytherura sp. 1

Pl. 14, fig. 10.

Diagnosis. A small, sub-quadrate species of *Amphicytherura* with well developed dorsal, median and ventral ribs, some cross-ribbing in anterior part of valve; entire lateral surface covered by fine pits.

Dimensions.	L	H
LV (MPK 11565)	0.45	0.27
RV (SAG 55)	0.43	0.26

Depository. MPK 11565

Material. 9 specimens.

Remarks. Very similar to *A. chelodon* in size and shape but differing in its pitted ornament, this species is probably new, but is left in open nomenclature due to the limited number of specimens. A thorough search through the material yielded no further specimens.

Range in this study. Upper Campanian to Lower Maastrichtian. This rare but distinctive species occurs sporadically in the basal *mucronata* Zone (Zone/subdivision 10) and Eaton Chalk (11) at Eaton, and in the Middle Weybourne Chalk (12) at Keswick. It is a rare component of assemblages in the Beeston Chalk (13) at Caistor-St-Edmunds and occurs in a single sample of the Paramoudra Chalk (14) at Whitlingham. It is present in the Lower Maastrichtian, but is restricted to a single sample in the Trimingham Grey Beds (18). It was not encountered in the Trunch Borehole.

Amphicytherura sp. 2

(not illustrated)

Diagnosis. A small, strongly reticulate species of *Amphicytherura* with a clear, hemispherical eye tubercle and a pronounced caudal process; anterior margin broadly rounded; posterior narrow, lower margin straight, upper surface concave.

Dimensions.	L	H
RV (SAG 79)	0.41	0.22

Depository. Assemblage slide 79

Material. 2 specimens.

Remarks. This species is rather similar to *Amphicytherura falloti* but is more strongly reticulate. It was left in open nomenclature due to its rarity.

Range in this study. Restricted to one sample (SAG 79) of the Upper Campanian Paramoudra Chalk, Crown Point Pit, Whitlingham.

Genus NIPPONOCYTHERE Ishizaki, 1971.

Diagnosis (Ishizaki, 1971, p. 88): "Carapace small, oblong. Sexual dimorphism pronounced. Posterior margin narrowly rounded at lower third. Surface with rather feeble reticulation. Narrow ventral marginal ridge (or crest) just along and above ventral margin. Eye tubercle not distinct. Hingement gongylodont; very thin. Marginal zone and vestibule rather broad in anterior margin. Adductor muscle scars in vertical row of 4, with a frontal scar heart shaped" (sic).

?Nipponocythere sp.

Pl. 15, fig. 11

Diagnosis. Small, oblong; posterior margin narrowly rounded; surface with feeble reticulation; ventral marginal rib narrow and very weakly developed.

Dimensions.	L	H
(MPK 11584)	0.48	0.26

Depository. MPK 11584

Material. A single specimen.

Remarks. Unlikely to be true *Nipponocythere*, erected by Ishizaki based on type material from the Recent of Japan, but the present author has found no other genus to which this specimen can be attributed. It does conform to several of the diagnostic features, but the hinge was obscured by adhering matrix. Some experiments with manual and chemical cleaning have been carried out by the present author to facilitate hinge examination, but this was not considered suitable for this fragile, thin shelled individual.

Range in this study. This specimen came from the Beeston Chalk of the Trunch Borehole (SAG 345).

Genus SCHIZOCYTHERE Triebel, 1950.

Treatise reference. Q331

Treatise diagnosis. (see also Van Morkhoven, 1963, pp 125-128):

"Carapace small to medium in size, ovate in side-view; posterior extremity being slightly angulated near middle, above which it is weakly concave in RV. Ovate in dorsal view; surface pitted to strongly reticulate, with distinct eye tubercle and in most species a tendency to have rib separating lateral and ventral surfaces. Hinge schizodont, in RV with split anterior tooth, deep socket divided into 2 parts at end, crenulate hinge furrow and lobed posterior tooth; anterior tooth bifid in LV. Marginal areas very broad, with about 5 straight radial canals on anterior part; normal canals rather large, widely spaced, sieve-like; muscle scars in somewhat curved row of 4 adductors, in front of which are single rounded antennal and mandibular scars very difficult to see."

Remarks. In the *Treatise*, the range of this genus is given as Eocene to Miocene. In the present study, one species is seen with clear *Schizocythere* characteristics, suggesting that the range should be extended back to the Lower Maastrichtian. The ornament of this species is smooth and shows more morphological variability than was originally described in the *Treatise*; it also shows a square caudal process not mentioned in Triebel's diagnosis. The genus *Paijenborchella* Kingma, 1948, ranges from the Upper Cretaceous to Recent in Europe and North America and differs in the presence of its long,

elongate caudal process and certain other details of ornament and internal structure. King (MS, 1968) considers the two genera in detail (pp. 281-286) in a discussion of the Schizocytheridae.

Schizocythere biponticulata sp. nov.

Pl. 15, figs 12-22.

Derivatio nominis: L. biponticulata - two bridged, from the bridge-like structures on the lateral surface.

Holotype. Female LV (MPK 11586)

Type level. SAG 2004, Lower Maastrichtian *Ostrea lunata* Chalk

Type locality. Marl Point, Trimingham, Norfolk.

Diagnosis. A medium species of *Schizocythere* in which median sulcus is not pronounced; ventral rib elongate, ventral margin rounded, dorsal margin convex, median rib short, bridge-like. Surface smooth; caudal process pronounced, short, square. Hinge strongly schizodont with crenulate median elements.

Description. Medium, thick-shelled; sub-ovate to sub-trapezoidal in lateral view; strongly inflated ventro-laterally in dorsal view and flattened ventrally. Sexually dimorphic, males more elongate and less strongly inflated than females. Anterior margin asymmetrically rounded with long, slightly convex antero-dorsal slope and much shorter, strongly convex antero-ventral slope; apex well below mid-height; posterior margin caudate, more pointedly so in males. Apex at or near mid-height; postero-dorsal slope concave, especially in males, postero-ventral slope straight, almost keel-like in some specimens. Dorsal margin with greatest height anterior of mid-length, sloping towards posterior. Ventral margin completely obscured by valve tumidity. Greatest length below mid-height; greatest height through dorsal umbo. Eye tubercle and ocular sinus absent. A deep vertical median sulcus occurs just anterior of mid-length, bridged by a short, median ponticulate rib and a longer, concave upward sub-ponticulate ventro-lateral rib which is strongly thickened medianly. A third rib borders the dorsal margin; intercostal areas smooth.

Inner lamella rather narrow, avestibulate; muscle scars obscured. Hinge schizodont with, in RV, a stepped anterior tooth increasing in height proximally anteriorly and a strongly bilobate posterior tooth; median element very strongly locellate posteromedianly with a strongly bi-loculate anteromedian socket; complementary structures occur in LV: long, gutter-like accommodation groove above median element.

Dimensions.	L	H
Holotype, female, LV (MPK 11586)	0.64	0.40
Paratype, female, LV (MPK 11585)	0.64	0.39
Paratype, male, LV (MPK 11587)	0.67	0.37
Paratype, female RV (MPK 11588)	0.65	0.39
Paratype, male, RV (MPK 11589)	0.68	0.37
Paratype, female, LV (MPK 11590)	0.63	0.39
Paratype, male, RV (MPK 11591)	0.65	0.39
Paratype, male, LV (MPK 11592)	0.68	0.36
Paratype, female, LV (MPK 11593)	0.64	0.39
RV juvenile from SAG 2004	0.60	0.34
LV juvenile from SAG 2001	0.58	0.32

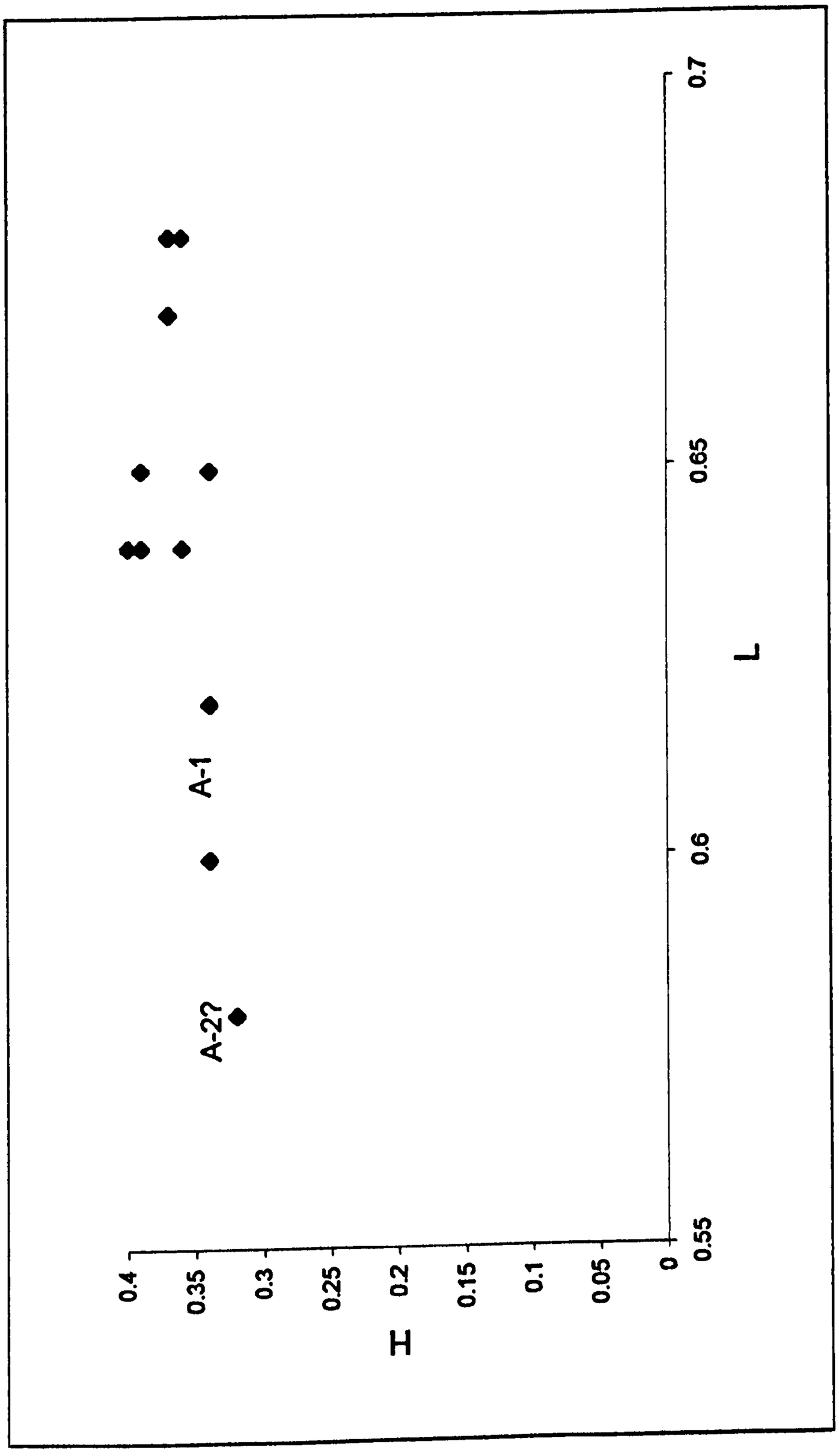


Fig. 2.3. Length - Height graph drawn for *Schizocythere biponticulata* sp. nov.

Length/Height: Sexual dimorphism is clear in this species, as illustrated in the L/H graph Fig. 2.3

Depository. MPK 11585 - 11593 and an assemblage slide containing an additional 20 specimens.

Material. 60 specimens.

Remarks. This species resembles *Paijenborchella marssoni* Triebel, 1949 (p. 199, pl. 2, fig. 13; pl. 3, fig. 14; see also Howe & Laurencich, 1958, p. 441 and Herrig, 1967, pl. 1, text fig. 4; King, 1968 MS), but there are several important differences. The genus *Paijenborchella* Kingma, 1948 (see also Triebel, 1950) is characterised by an elongate caudal process, a well-developed median sulcus and certain other details of morphology. In *Paijenborchella marssoni,* the caudal process is narrow and extremely elongate; in the present species, this structure is short and square (less than half the length). The median sulcus is also less pronounced and the new species is larger (ranging from 0.63 to 0.68mm; Triebel records specimens which are on average only 0.50mm long. The specimens illustrated by King (MS, 1968) from the British Lower Maastrichtian are not conspecific with Triebel's species; they are much closer to *S. biponticulata* sp. nov. and could probably be incorporated into it. The present author has not done this, however, since King's original specimens or those of Triebel have not been examined.

Range in this study. This distinctive species is entirely restricted to the Lower Maastrichtian *O. lunata* and Grey Beds of Trimingham (SAG 2001 to 2010), where it comprises between 0.7 to 7.6% of assemblages. it is, therefore, a possible marker species for the Lower Maastrichtian at its type locality and was used to erect the *S. biponticulata* Range Biozone. It reaches a maximum abundance in SAG 2004 (*O. lunata* Chalk, 23 specimens recovered, including the holotype).

Family PROTOCYTHERIDAE Ljubimova, 1955

Subfamily PROTOCYTHERINAE Ljubimova, 1955

Genus PROTOCYTHERE Triebel, 1938.

Treatise reference. Q327

Treatise diagnosis. "Carapace elongate, LV much larger than RV; surface with 3 longitudinal ridges or swellings. Hinge antimerodont; marginal areas broad, long radial pore canals upturned in upper part of anterior end; muscle scars in vertical row of 4, with heart-shaped antennal scar in front. *U. Jur.-L. Cret.*".

Weaver, 1982, p. 54. "Left valve larger than right with distinct hinge ear. Valves with 3 longitudinal ribs. Hinge strongly merodont. Marginal pore canals long, arched upwards in upper half of anterior margin."

? Protocythere sp.?

Pl. 17, figs 1-2

Diagnosis. An elongate species tentatively placed in *Protocythere*. Anterior margin smooth and broadly rounded; posterior narrow; longitudinal ridges present, median rib being especially clear, ventral rib obscuring ventral margin, dorsal rib slightly reduced. Intercostal areas weakly reticulate.

Dimensions.	L	H
MPK 11635	0.45	0.19

Depository. MPK 11635

Material. 1 specimen.

Remarks. This specimen is placed tentatively in *Protocythere* due to the strong resemblance to Lower Cretaceous protocytherids especially in the 3 longitudinal ribs, but this cannot be proven due to the rarity of this species in the present study. The hinge was obscured by adhering matrix and the specimen was considered too fragile for manual or chemical cleaning.

Contrary to prior opinion, the family Protocytheridae did not become extinct in the Cretaceous, as witnessed by the occurrence in modern deep-sea assemblages of such genera as *Abyssocythereis* Schornikov. This is represented throughout the Tertiary, always in deep-sea environments by a single species (pers. comm. Prof. R. Whatley, April 2000).

Range in the present study. Upper Campanian Paramoudra Chalk, Thorpe.

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948
Subfamily BRACHYCYTHERINAE Puri, 1954.

The problems associated with Pterygocytherid taxonomy and recognition.

Blake (1933) originally described *Pterygocythereis* as including species that are "triangular in dorsal view, produced by the pronounced alae along the ventro-lateral valve." Murray & Hussey, 1942, describe the genus *Alatacythere* to include species differentiated from those assigned to *Pterygocythereis* by a "crenulate posterior terminal element on the right valve." Hill, 1954, erected *Pterygocythere* to include strongly alate species with Brachycythere-type hinges. Van Morkhoven, 1963, considered *Pterygocythere* and *Alatacythere* as junior synonyms of *Pterygocythereis* with two subgenera:

a) *Pterygocythereis (Pterygocythere)* with a *Pterygocythere* shape but with a crenulate posterior tooth and an accommodation groove in the LV.

b) *Pterygocythere (Pterygocythere)* with a knob-like posterior tooth and no accommodation groove in LV, dorsal margin in this is also arched.

Weaver, 1982, follows Van Morkhoven, but includes *Pterygocythereis* in the Brachycytherinae.

Wilkinson (1988a, MS, p. 378) makes the following observations:

1) *Pterygocythereis* has a holoamphidont hinge; there is no accommodation groove; lateral surface is spinose especially along the dorsal margin and ala. It should be placed within the Trachyleberidinae.

2) *Alatacythere* has a hemiamphidont hinge with a crenulate median groove and a small, narrow accommodation groove in the left valve. It is laterally alate, but non-spinose except at the end of the alae. It should, therefore, be placed in the Brachycytherinae.

3) *Pterygocythere* has a hemiamphidont hinge with a smooth median element and a well-formed accommodation groove in the left valve. It is not spinose, except at the end of the alae. It should be placed in the same family as *Alatacythere* but Wilkinson considers it to be a junior synonym of the latter genus.

Majoran (1989) notes that there are differing opinions on whether *Pterygocythere* should be considered as a sub-genus of *Pterygocythereis* (following Weaver, 1982 and other authors) or as a separate genus (following Babinot, 1980). Majoran concludes that the latter is correct. The present author agrees. Puckett (1996, p. 76) brings the taxonomy more up to date and places the genus

Pterygocythereis in the subfamily Pterygocytherideinae Puri, 1957 (following Hazel, 1967a, 1967b), while also following the subgeneric and generic classifications of Van Morkhoven.

Working with the classification as it will appear in the *Treatise* revision (pers. comm. Prof. R. Whatley, July 1999), *Pterygocythere* and *Alatacythere* are here placed within the family Trachyleberididae, subfamily Brachycytherinae (in the 1961 *Treatise*, they are classified in the Brachycytheridae Puri, 1954). *Pterygocythereis* will appear later in this systematic taxonomy, in the subfamily Trachyleberidinae (in the old *Treatise*, this genus is still included in the Brachycytheridae).

Genus ALATACYTHERE Murray & Hussey, 1942.

Treatise reference, Q260-261

Treatise diagnosis. "Identical in all essential features except hinge to *Pterygocythereis*. Hinge hemiamphidont, with very narrow accommodation groove over median bar of LV in type species. [Might well be considered a subgenus of *Pterygocythereis*, but differs in range.] *U. Cret.-Oligo.*

Wilkinson, 1988a (MS). "Laterally alate, but not spinose except at the end of the alae."

Alatacythere robusta (Jones & Hinde, 1890).

Pl. 16, figs 1-6.

1849 *Cythereis alata* (Bosquet). Jones, p. 21, pl. 4, figs 14a-d.

1890 *Cytheropteron alatum* (Bosquet) *robusta* Jones & Hinde, p. 35, pl. 2, figs 24-27.

1941 *Brachycythere lünensis* Triebel, p. 336, pl. 8, figs 78-79,

non pl. 8, figs 80, 77b = *Alatacythere robusta fortis*

1954 *Diogmopteron lünensis* (Triebel). Hill, pp 824-825, pl. 98, fig. 9a; pl. 100, figs 3a-b

1958 *Diogmopteron lünensis* (Triebel). Howe & Laurencich, pp 319-320.

1958 *Pterygocythere? robusta* (Jones & Hinde). Howe & Laurencich, p. 484.

1964a *Alatacythere robusta* (Jones & Hinde). Kaye, p. 51, pl. 2, figs 7-11, 13-16, 18.

1966 *Diogmopteron alatoides* (Bonnema). Herrig, pp 832-833; pl. 24, figs 5, 6.

1968 *Diogmopteron robusta* (Jones & Hinde). King, MS, pp 266-270; pl. 29, figs 1-4; pl. 30, fig. 1.

1978 *Alatacythere robusta* (Jones & Hinde). Neale, pl. 15, figs 11-14.

?1982 *Pterygocythereis (Pterygocythere)* cf. *P. (P.) robusta* (Jones & Hinde). Weaver, pl. 10, figs 6-7.

Diagnosis. A medium-large species of *Alatacythere* distinguished by its square outline; anterior margin rounded and denticulate; posterior margin spinose; alar process spinose on trailing edge; smooth and relatively heavily calcified.

Dimensions.	L	H
LV (MPK 11594)	0.76	0.46
LV (MPK 11595)	0.73	0.44
RV (SAG 389)	0.75	0.46

Depository, MPK 11594-11599; additional specimens curated on species slide.

Material. More than 100 specimens.

Remarks. This species was originally referred by Jones, 1849, and Jones & Hinde, 1890, to *Cythere alata* of Bosquet, but its squarer outline and denticulate margin characterise it as a separate species. The material of the present study closely resembles that of Neale (1978) in all aspects except one: the posterior margin bears only a few short spines, while in Neale's figures, the posterior margin has at least 4 prominent spines. Some specimens do, however, show this "marked postero-ventral spination." Weaver's *Pterygocythereis (Pterygocythere) cf. P. (P.) robusta* from the British Cenomanian is, in this study, considered to be conspecific, differing only in the "short dorsal rib in the LV and a distinct accommodation groove." The species is extremely variable, as noted by Kaye, 1964, and the exact position of the Cenomanian forms cannot by fully ascertained.

Triebel's *Brachycythere lünensis* (the present author reproduces the exact usage in the above synonymy but it should be noted that the ICZN -International Code on Zoological Nomenclature- rules against the use of diacritic marks in species names) from the Lower Senonian of Germany is, in part, assigned to *A. robusta.* Triebel's species was later used by Hill, 1954 and Howe & Laurencich, 1958, under the generic name *Diogmopteron.* In the present study, all three references appear in synonymy with *A. robusta* of Jones & Hinde, 1890. King (1968, MS, pp 266-270) also uses this genus and discusses it in some detail. The genus *Diogmopteron* Hill, 1954 (old *Treatise,* 1961, Q 263-264), restricted entirely to the Upper Cretaceous of Europe, was placed by Weaver, 1982, into *Pterygocythereis* (sensu lato). Weaver (p. 58) considers that "the presence of an accommodation groove in the right valve instead of the left is thought to be insufficient to warrant generic or subgeneric status." The present author agrees with this but the genus does not belong in *Pterygocythereis.* In the *Treatise* revision, *Diogmopteron* will probably be considered synonymous with *Alatacythere.*

Wilkinson & Morter, 1982, report *Alatacythere robusta langi* Kaye from the East Anglian Gault (pl. 13.2, fig. 11). This subspecies is very like *A. robusta* but the posterior spines are longer and more elongate. The RV of *Pterygocythere rati* Damotte, 1971a, as illustrated by Babinot *et al.,* 1985 (pl. 58, fig. 6) is similar in shape but is more elongate.

Pterygocythereis (Pterygocythere) diminuta Weaver, 1982 (p. 58, pl. 10, figs 9-11) from the British Upper Cenomanian is similar to *Alatacythere robusta* in shape, but is much smaller and the RV overlaps the LV. In the latter species, the LV overlaps the RV along the dorsal margin

Published range. In Britain, the species is recorded from the Cenomanian and Turonian (e.g. Weaver, 1982; Slipper, 1996), but is most common in Santonian to Maastrichtian intervals. Jones & Hinde, 1890; King (1968, MS) and Neale, 1978, record it from the Norwich Chalk. King, in a systematic study of selected British Upper Chalk Ostracoda, records the range for this species (1968, MS, p. 269) as *Uintacrinus* Zone (Santonian) to Lower Maastrichtian, noting its abundance in the Upper Campanian and Lower Maastrichtian of Norfolk and Northern Ireland.

Range in this study. The species is long ranging in Norfolk; occurring from the Coniacian to Lower Maastrichtian. This represents a slight extension in the stratigraphical range for this common and distinctive species. It first appears, in the outcrop samples, in the uppermost samples of the Coniacian basal *coranguinum* Zone and also in the low *coranguinum* and *coranguinum* zones (zone/subdivisions 1-3) at Euston, Suffolk and South Pickenham, Norfolk. It is, however, not present in the Santonian and only occurs in the uppermost samples of the Lower Campanian (SAG 181, 182) at Bawburgh, Norfolk

(zone/subdivision 9). It is significantly more abundant in the Upper Campanian to Lower Maastrichtian. In the Upper Campanian, it occurs in the basal *mucronata* and Eaton chalks (10, 11) at Eaton, Norfolk and in all but one of the Middle Weybourne Chalk (12) samples from Keswick. It is also present in the Beeston Chalk (13) at Caistor St Edmunds. In the Lower Maastrichtian, the species occurs in the pre-*Porosphaera* Beds (15) of Sidestrand and the Grey Beds at Trimingham.

In the Trunch Borehole, it has a more restricted range (Lower Campanian - Lower Maastrichtian). It first appears in the lower part of the Lower Campanian *Gonioteuthis quadrata* Zone (FAD SAG 544) and extends into the top sample of the Lower Maastrichtian *Porosphaera* Beds (SAG 213).

Alatacythere robusta fortis (Jones & Hinde, 1890)

Pl. 16, fig. 7-14

1890 *Cytheropteron alatum* (Bosquet) var. *fortis* Jones & Hinde, p. 36, pl. 2, figs 20, 21.

1940 *Brachcythere lünensis* Triebel, p. 336, pl. 8, figs 80, 77 (*non* figs 78, 79 = *Alatacythere robusta*).

1964 *Alatacythere robusta fortis* (Jones & Hinde). Kaye, pl. 2, fig. 12.

Diagnosis. A large, sub-rhomboidal to sub-quadrate species of *Alatacythere* with strong antero-ventral and postero-ventral marginal denticles; marginal rim strongly developed and extending around entire periphery in RV but absent mid-dorsally in LV. Alar projection strongly developed, backwardly curving and wing-like, obscuring ventral margin.

Dimensions.	L	H
Female RV (MPK 11600)	0.71	0.46
Male LV (MPK 11601)	0.73	0.45
Female RV (MPK 11602)	0.73	0.45

Depository. MPK 11600-11607

Material. 40 specimens.

Remarks. The present material is identical to that illustrated by Jones & Hinde but significantly smaller (Jones & Hinde give measurements of L 1.0mm, H 0.48mm). It is also slightly more inflated (dorsal margin also more strongly arched) than the specimen (pl. 2, fig. 12) illustrated by Kaye, 1964a. Kaye, 1964a (p. 51) includes both the nominative and the subspecies in synonymy, noting that the "available specimens of this species show that there is an inter-gradation between most of Jones & Hinde's varieties. The degree of inflation, the size and shape of the ala, the arching of the dorsal margin and the denticulation of the anterior and posterior margins is extremely variable; all intermediates being seen to occur. A thorough statistical study of a large number of specimens may, however, enable the species to be subdivided." In the present study, the two forms do differ sufficiently to facilitate such a division. King (1968, MS) also includes *A. robusta fortis* in synonymy with the nominative species but several illustrated specimens conform more closely to the subspecies.

The RV of *Pterygocythere rati* Damotte, 1971a, figured by Babinot *et al.*, 1985 (pl. 58, fig. 6) is similar in shape to *A. robusta* and *A. robusta fortis* but has a more elongate posterior and a more spinose anterior margin. The LV is different in shape (pl. 58, fig. 7). *Pterygocythere pulvinata* Damotte, 1962, (pl. 6, fig. 2), also illustrated by Babinot *et al.*, 1985 (pl. 58, figs 8, 9) is similar in LV specimens but RV are

more elongate and narrower; the ventro-lateral ala is less pronounced in RV specimens and these appear more like *A. robusta.* Both valves are smaller than *A. robusta fortis* and the anterior margin is more elongate and acute. *Pterygocythereis (Pterygocythereis) asserulata* (Bonnema), illustrated by Damotte, (1971a, pl. 6, fig. 3; 1971b, pl. 6, figs 35, 36) from the French Upper Campanian is a larger species with a stronger ventrolateral alae.

Published range. Rare in published records; restricted to the Chalk of Norwich and Northern Ireland.

Range in this study. The illustrated specimens come from SAG 2017, Lower Maastrichtian pre-*Porosphaera* Beds (between flint bands T and S). The species is most common in the Lower Maastrichtian and ranges from the Upper Campanian upwards. It first appears in the outcrop samples in the basal *mucronata* Chalk (10) at Cringleford and Eaton. It is present also in the Middle Weybourne Chalk (12) at Keswick. It occurs in a single sample (SAG 51) of the Beeston Chalk (13) at Caistor-St Edmunds. In the Trunch Borehole, the range is more restricted and the species only occurs in the upper parts of the Upper Campanian Weybourne and Beeston chalks.

A note on the origins of *Pterygocythere* and *Pterygocythereis*. Both *Pterygocythere* and *Pterygocythereis* derive from a hemi-amphidont *Alatacythere* of uncertain origins (Guernet, 1990) at the end of the Lower Cretaceous. *Pterygocythereis* is Cenomanian to Recent in its range and the genus evolved by the modification of general form and re-enforcement of the hinge structure.

Genus PTERYGOCYTHERE Hill, 1954

Treatise reference. Q 267

Diagnosis. "*Pterygocythere* has a hemiamphidont hinge with a smooth median element and a well formed accommodation groove in the left valve. It is not spinose, except at the end of the alae", Wilkinson, 1988, MS.

Pterygocythere hibernica (Jones & Hinde, 1890)

Pl. 16, fig. 15.

1890 *Cytheropteron hibernicum* Jones & Hinde, pp 36-37; pl. 2, figs 22, 23.

1964a *Alatacythere robusta* (Jones & Hinde)*hibernicum*. Kaye, pl. 2, fig. 14.

1964 a *Alatacythere robusta* (Jones & Hinde)*?hibernicum*. Kaye, pl. 2, fig. 16.

1968 *Pterygocythere hibernica* (Jones & Hinde). King, MS, pl. 29, figs 5, 6.

1978 *Pterygocythere hibernica* (Jones & Hinde). Neale, pl. 15, figs 15-17; pl. 16, figs 1-2.

Diagnosis. A large, rounded, sub-quadrate species of *Pterygocythere*; broad, smooth and convex; anterior margin broadly rounded with only a few weak spines; ventral margin straight and overhung by a long, broad, angular wing-like alar process terminating in a long spine; posterior margin depressed, narrow and truncate with 3 short spines.

Dimensions.	L	H
LV (MPK 11608)	0.85	0.55

Depository. MPK 11608 and SAG 345

Material. 2 specimens

Remarks. The material of the present study is identical to that illustrated by Jones & Hinde, 1890 and Neale, 1978. They are also very similar to material illustrated by King, 1968 MS, but are larger (0.85 mm in length, compared to 0.78mm). Kaye illustrates two specimens which are identical to the present material and are both considered to be conspecific with Jones & Hinde's original species.

Published range. The species is rare in published records and restricted to the Santonian to Campanian of the British Isles. Jones & Hinde record it from the Chalk of Antrim, Northern Ireland. Kaye, 1964a and Neale, 1978, illustrate specimens from the Antrim Chalk and Norwich. King, 1968, MS, illustrates specimens that, although identical (except for their smaller size), differ from the present material and previously published records in stratigraphical range. He illustrates six specimens from the *coranguinum* Zone of Kent and from the Lower Campanian *Gonioteuthis quadrata* Zone of the Isle of Wight.

Range in this study. This species is rare in the present study, restricted to the Upper Campanian Beeston Chalk of the Trunch Borehole. It is used in the biozonation to erect the *Pterygocythere hibernica* Range Biozone but, due to the rarity of the species, this should be used with caution.

Pterygocythere laticristata (Bosquet, 1854)

Pl. 16, figs 18-21.

1854 *Cythere laticristata* Bosquet, p. 118, pl. 7, fig. 11a-d.

1940 *Brachycythere laticristata* (Bosquet). Bonnema, pl. 4, figs 5-7.

1958 *Brachycythere laticristata* (Bosquet). Howe & Laurencich, pp 86-87.

1964a *Brachycythere laticristata* (Bosquet). Kaye, pl. 2, figs 1-4, 6.

1968 *Pterygocythere laticristata* (Bosquet). King, MS, pl. 29, figs 7-9.

1978 *Pterygocythere laticristata* (Bosquet). Neale, pl. 16, figs 3-13.

1982 *Pterygocythereis (Pterygocythere)* cf. *P. (P.) laticristata* (Bosquet). Weaver, p. 59, pl. 10, figs 3-5.

1985 *Pterygocythere laticristata* (Bosquet). Robaszynski *et al.*, p. 109, pl. 20. figs 7-9.

1988 *Pterygocythereis laticristata* (Bosquet). Bless & Robaszynski, text fig. 2, pl. 1, fig. F.

Diagnosis. A heavily calcified and strongly inflated species with a short, blunt alar process; dorsal margin weakly rounded in LV, straight in RV. Eye tubercle is small. Posterior margin pointed with a straight upper surface and a convex, slightly lower surface; anterior margin broadly rounded.

Dimensions.	L	H
RV (MPK 11611)	0.82	0.52
LV (MPK 11612)	0.85	0.54
RV (MPK 11613)	0.88	0.58
RV (MPK 11614)	0.86	0.54

Depository. MPK 11611 - 11614 and various assemblage slides.

Material. At least 50 specimens.

Remarks. The typical, strongly alate species of *Pterygocythere* and *Pterygocythereis* are easily distinguished by their hinge structure, but less alate forms may be mistaken for *Brachycythere*. This explains why both Bonnema (1940) and Kaye (1964a) referred the species to *Brachycythere*. Weaver

(1982, p. 59) assigns his specimens to *Pterygocythereis (Pterygocythere)* referring the species to that of Bosquet. The Cenomanian specimens are identical to those of the Campanian to Maastrichtian and only differ in that the dorsal margin in the LV is not as strongly arched. They are, however, almost certainly synonymous; any slight variations being due to the development of the species. The present study follows Neale (1978) in assigning the species to *Pterygocythere*, since it possesses a clearly hemiamphidont hinge with a smooth median element and an accommodation groove in the LV.

Pterygocythere rati Damotte, 1971 (pl. 6, fig. 1), also illustrated by Babinot *et al.,* 1985, differs from *P. laticristata* by its smaller size and narrow anterior margin, with 3 prominent spines, spinose posterior and more elongate shape. In the latter species, the posterior is broadly rounded and the ventro-lateral alae is broad and blunt; in Damotte's species this feature is narrower and less prominent. *Pterygocythere* cf. *allinensis* (Grekoff & Deroo, 1956) illustrated by Babinot, 1980, (pl. 12, fig. 16; pl. 13, fig. 1) from the French Middle Turonian is very similar in shape with an arched dorsal margin, rounded anterior margin and prominent alae but the posterior is more narrow, elongate and acute. In *P. laticristata,* the posterior is broader, less drawn out and more broadly rounded.

King, 1968, MS, notes that there is a characteristic stratigraphical size increase in the Upper Campanian basal *mucronata* Chalk - length average 0.80mm, Eaton Chalk, 0.89mm. Lower Maastrichtian - 0.95mm. The specimens in the present study are of a similar size (0.82-0.86mm) to King's Upper Campanian material but there was no difference between individuals from Upper Campanian samples and those from the Lower Maastrichtian.

Robaszynski *et al.,* 1985, working on the Campanian-Maastrichtian boundary in the chalky facies close to the type Maastrichtian, illustrate several specimens of *P. laticristata* which differ from the present material only by a slightly more strongly arched dorsal margin in the LV. Both the 1985 material and that of the present study can, however, be considered synonymous with Bosquet's original species.

Published range. In Britain and Europe, the published range is Upper Campanian to Maastrictian (King, 1968, MS; Neale, 1978) but this has now been extended. Weaver, 1982, records specimens considered conspecific with *P. laticristata* from various localities in the British Cenomanian while Johnson, 1996, records *P.* cf. *laticristata* from the Plenus Marls of the Isle of Wight. Bless & Robaszynski, 1988, record the species from the Lower Campanian Vaals Greensand of Northeastern Belgium and the Maastrichtian of South Limburg. It was also recorded from the Campanian to Lower Maastrichtian chalky facies of the type Maastrichtian. The species is well documented in the Chalk of Norfolk (Kaye, 1964a; King, 1968, MS; Neale, 1978; this study) and Bonnema (1940) recorded it from the Chalk of the Netherlands.

Range in this study. In the present study, *Pterygocythere laticristata* ranges from the upper part of the Lower Campanian to Lower Maastrichtian.

It is slightly less common in the outcrop assemblages, compared to those of the Trunch Borehole, but exhibits a similar range. It first occurs in the Lower Campanian in the highest samples of the *Gonioteuthis quadrata* Zone (9) and in the Upper Campanian basal *mucronata* Chalk (10) and Weybourne Chalk (12). It is a Lazarus taxa throughout the higher zones of the Upper Campanian (Beeston and Paramoudra chalks - zone/subdivision 13, 14), reappearing in the Lower Maastrichtian. In the Lower Maastrichtian, it occurs in the pre-*Porosphaera* Beds of Sidestrand and Grey Beds of Trimingham (15 and 18 respectively). In the Trunch Borehole, the species first appears in the Lower

Campanian *G. quadrata* Zone (FAD SAG 534) and extends up into the Lower Maastrichtian pre-*Porosphaera* Beds (LAD SAG 217).

Genus BRACHYCYTHERE Alexander, 1933

Treatise reference. Q260

Treatise diagnosis. "Carapace subtriangular to subovate in lateral view, plump ventrally, usually with small carina separating flattened ventral face from lateral face; ventral surface usually striated longitudinally, lateral surface smooth-weakly reticulate; eye spot distinct; anterior end broadly and obliquely rounded, posterior end subangulate at or below middle. Hinge hemiamphidont. *U. Cret.-Rec.*"

Brachycythere sp.

Pl. 16, figs 16-17.

Diagnosis. A large, sub-ovate and inflated species of *Brachycythere*; smooth and thickly calcified; anterior margin broadly rounded. Dorsal margin strongly arched, ventral margin strongly convex; posterior narrow. Hinge well developed; hemiamphidont.

Dimensions.	L	H
RV (MPK 11609)	0.89	0.60
RV (MPK 11610)	0.92	0.62

Depository. MPK 11609-11610

Material. 4 specimens.

Remarks. Rather similar to *Pterygocythere laticristata* but much more inflated, larger and differing in the details of the hinge and internal area. The present material is very similar to *Brachycythere* sp. 1 from the Middle Eocene, offshore Florida, illustrated by Guernet & Bellier, 2000 (p. 268, pl. 4, fig. 8) and several other published species from the Cretaceous.

Range in this study. This species is very rare in the present study and restricted in its stratigraphical range. In the Upper Campanian, it occurs in a single sample of the Trunch Borehole (SAG 345, Beeston Chalk, Upper Campanian) and in one sample from the Beeston Chalk (SAG 52) at Caistor St Edmunds. It is, however, slightly more abundant in the Lower Maastrichtian of the Trunch Borehole, where it occurs in the pre-*Porosphaera* Beds (SAG 231) and *Porosphaera* Beds (SAG 213).

Family TRACHYLEBERIDIDAE Sylvester-Bradley, 1948.

Genus CORNICYTHEREIS Gründel, 1973

Diagnosis, Weaver, 1982, p. 60. "Valves small to moderate in size. Hinge ear small and rounded. Lateral surface smooth, longitudinal ribs not divided into spines. Muscle nodes low and joined to middle rib. Valves moderately inflated."

Table 2.2.: GENUS *CURFSINA* DEROO, 1966

type species *Curfsina major* Van Veen 1936

	original type description, Deroo, 1966	Weaver,1982, p. 62
eye tubercle	present, hemispherical on frontal lobe, with ocular ridge	present, rather large
size, shape, ornament	moderate to small, reticulate ornament; intercostal surfaces smooth or irregularly ornate, ridged, reticulate, spinose, punctate	hinge ear weak to absent, size moderate to small, ornament reticulate, smooth or pitted
anterior marginal rib	present, behind ocular tubercle	present, sometimes bearing elongate pits (as in C. derooi Weaver, 1982)
dorsal rib	present	present, rarely divided into spines, often with vertical processes at their posterior ends
subcentral tubercle	circular to longiform and may or may not be joined to median rib	rounded or slightly elongate
median rib	present	joined or separate from subcentral tubercle
ventrolateral rib	may join anterior rib	rarely divide into spines, often with vertical processes at their posterior ends
hinge	amphidont, in RV long anterior tooth, smooth median element. elongate, crenulate posterior tooth	in C. derooi, hinge in RV consists of a "long, peg-like anterior tooth which may be weakly lobed; deep, rounded anteromedian socket, smooth median groove and elongate,weakly crenulate posterior tooth = hemiamphidont/holamphidont
marginal zone, muscle scars	4 adductors and a v-shaped antennal scar; inner lamella and marginal zone moderately broad with a number of marginal pore canals	inner lamella moderately broad, avestibulate; marginal pore canals difficult to see, at least 15 anterior MPC; scars not mentioned - as in original diagnosis.

Family : TRACHYLEBERIDIDAE Sylvester-Bradley, 1948

Subfamily: TRACHYLEBERIDINAE Sylvester-Bradley, 1948.

Genus CORNICYTHEREIS

Cornicythereis sp.

Pl. 17, figs 3-4.

Diagnosis. A medium, relatively strongly calcified species, sub-triangular in shape, tapering towards posterior; anterior margin rounded; sub-central tubercle joined to median rib; lateral area smooth.

Dimensions.	L	H
MPK 11636	0.68	0.38

Depository. MPK 11636, 11637

Material. 2 specimens.

Range in this study. Restricted to a single sample from the Lower Maastrichtian at Overstrand (SAG 2)

Genus: CURFSINA Deroo, 1966.

Generic diagnosis. This is tabulated in table 2.2.

Weaver, 1982, p. 62: "Carapace of small to moderate size. Hinge ear weak to absent. Dorsal and ventral ribs rarely divided into spines, often with vertical processes at their posterior ends. Middle rib joined to or separate from muscle node. Surface with reticulation, pits or occasionally smooth."

Curfsina ceraunos sp. nov.

Pl. 17, figs 5-20.

Derivatio nominis:: Gr. κεραυνοζ - keraunos, a thunderbolt or stone supposed to have fallen from the sky, from the fanciful resemblance of the surface ornament to that of a stony meteorite.

Holotype. Female left valve (MPK 11638)

Type level. SAG 377, Upper Campanian Weybourne Chalk

Type locality. Trunch Borehole, Norfolk.

Diagnosis. A medium species of *Curfsina* characterised by its distinct ornament; anterior part of lateral surface covered with very small, regular puncta; area behind large sub-central tubercle comprising several deep, rectangular pits.

Description. Medium. Subquadrate in lateral view, when complete carapaces viewed dorsally, two prominent, spherical tubercles seen on anterior part of the dorsal margin. Anterior margin broadly rounded with 4-5 short spines in the LV, 3 in RV; apex at about mid-height; thick anterior rib in both valves. Dorsal margin straight, slightly shorter in RV, with three short dorsal spines and a small postero-dorsal process; ventral margin straight, spinose with a larger postero-ventral spine at about two-thirds

length, a shorter spine behind this situated directly below the postero-dorsal spine; posterior narrow, elongate, acute, apex at mid-height, with thick marginal rib. Large eye tubercle connected to anterior marginal rib and joined to the large boss-like sub-central tubercle (at about two-thirds length) by a short, straight rib; a second rib of equal size and thickness connects this tubercle with the antero-ventral part of the valve but this does not reach the anterior marginal rib. Sub-central tubercle is slightly larger in LV specimens, especially in females. Sexual dimorphism pronounced; males longer; anterior margin more spinose, females less elongate, broader and more inflated, dorsal margin slightly shorter and less spinose. Earlier stage juveniles are entirely punctate, later stage juveniles more closely resemble adult ornament. Sub-central tubercles and marginal and posterior ribs, eye tubercle and postero-dorsal and postero-ventral processes evident at an early stage of development. Anterior part of valve covered with very small, regularly spaced puncta grouped into sub-rectangular arrangements, 9-12 in each group; area behind the large, smooth sub-central tubercle comprising several deep, rectangular pits which are especially clear in LV, more irregular in RV; anterior and posterior marginal ribs smooth with a narrow area behind this rib which is also smooth. Posterior area behind the rectangular pits and in front of the posterior marginal rib with small circular puncta similar to those of the anterior area.

Sub-central tubercle distinct and hollow in internal view; marginal zone moderately broad, widest at anterior, avestibulate; marginal pore canals indistinct, few, widely spaced, straight and simple. Hinge strongly developed, holamphidont; hinge line straight; RV consisting of a circular, deep antero-median socket, a smooth or weakly lobed, peg-like anterior tooth; smooth, straight median element and an elongate, weakly crenulate posterior tooth. LV complementary. Other internal features not seen.

Dimensions.	L	H
Holotype, LV female (MPK 11638)	0.66	0.40
Paratype, LV male (MPK 11639)	0.70	0.38
Paratype, LV male (MPK 11640)	0.70	0.37
Paratype, LV male (MPK 11641)	0.72	0.37
Paratype, RV female (MPK 11642)	0.66	0.41
Paratype, LV female (MPK 11643)	0.62	0.39
Paratype, LV female (MPK 11644)	0.66	0.41
Paratype, RV male (MPK 11645)	0.69	0.38
Paratype, RV female (MPK 11646)	0.64	0.40
Paratype, RV female (MPK 11647)	0.66	0.40
Paratype, C male (MPK 11648)	0.69	0.38
Paratype, C female (MPK 11649)	0.66	0.40
Paratype juv. RV (MPK 11650)	0.57	0.28

Depository. MPK 11638 to 11650

Material. More than 150 specimens.

Remarks. In the present material, two distinct sub-forms can be identified based on differences in size, ornament and stratigraphical range. Form α is slightly larger, more elongate and conforms to the species diagnosis and description; the ornament is distinctive; tiny regular puncta on the anterior lateral surface;

a large sub-circular sub-central tubercle and several deep regular (more irregular in the RV) pits on the posterior lateral surface behind the sub-central tubercle. Juveniles show a more spinose ornament but, even in the early instars, the anterior and posterior marginal rims and the large sub-central tubercle is evident (e. g. MPK 11650 of this study). Form β is smaller, characterised by a broader anterior margin which is less spinose than in form α and, in the LV, has 7-8 small, round tubercles.

Pokorny, 1967, describes species from the Lower Turonian-Upper Coniacian of Czechoslovakia. *Curfsina senior* (pl. 1, figs 1, 2; pl. 3, figs 1, 5; text fig. 1A, 1F, 2) from the Lower Turonian has a similar shape and ornament; it is also closer to the present material in size, but is more heavily calcified. The eye tubercle is more prominent; the anterior marginal rib is thicker and the margin more spinose, the ventrolateral spine is larger and the posterior ornament behind the large sub-central tubercle is more regular and the pits are larger. *Curfsina kafkai kafkai* is similar in shape to the present species, but is smaller and characterised by its lack of ornament. *Curfsina subparva* (pp. 355-61; pl. 3, figs 6-7; pl. 4, figs 2, 3) is a smaller species, with a regular reticulate ornament covering the entire lateral surface.

Weaver describes and illustrates *Curfsina derooi* from the Upper Cenomanian of Dorset (pl. 11, figs 1-4, p. 62). This is similar to the present material in shape but is smaller and differs in its ornament (reduced dorsal and median ribs; ornament less punctate, lacking the deep rectangular pits of *C. ceraunos)*. The latter species also differs from *Curfsina? decorata decorata* Donze, 1972, from the French Cenomanian in its less pointed posterior and different ornament.

Range in this study. Form α occurs in the Lower Campanian to Lower Maastrichtian in the Trunch Borehole (First Appearance SAG 602, Lower Campanian *O. pilula* Zone, Last Appearance SAG 217, Lower Campanian pre-*Porosphaera* Beds). In the outcrop samples, it is slightly more restricted. The more common α-form is present in the Upper Campanian basal *mucronata*, Eaton, Weybourne, Beeston and Paramoudra chalks (10-14) and in the Lower Maastrichtian pre-*Porosphaera* Beds of Sidestrand and in the *O. lunata* Chalk and Grey Beds of Trimingham (15, 17, 18 respectively). Form β is restricted to the Lower Maastrichtian Grey Beds of Trimingham and does not occur in the Trunch Borehole.

Curfsina sp. cf. *C. kafkai kafkai* (Pokorny, 1967)

Pl. 18, figs 1-6.

cf. 1967 *Curfsina kafkai kafkai* Pokorny, p. 350-3; pl. 1, fig. 3; pl. 2, fig. 1; pl. 3, fig. 2; text figs 1C-E, 1G).

Diagnosis. A small sub-species of *Curfsina kafkai* with a large postero-dorsal tubercle and small tubercles along the dorsal margin, and a pronounced "break" in its sub-alar ventro-lateral rib posteriorly. Intercostal areas minutely punctate. Hinge holamphidont.

Dimensions.	L	H
LV male (MPK 11653)	0.61	0.29
LV female (MPK 11655)	0.54	0.32
RV female (MPK 11656)	0.53	0.32
RV male (MPK 116657)	0.57	0.27

Depository. MPK 11653-11658

Material. More than 100 specimens.

Remarks. The different stratigraphical range of this species should be noted; the present material is similar to Pokorny's species but can only be compared to it due to a slight difference in size and shape and ornament. The material of the present study is less heavily calcified and shows only fine puncta which is variable and is not evident on all specimens. The species is similar in shape to *Curfsina ceraunos* sp. nov., but is slightly smaller and characterised by its lack of ornament. The latter has a distinctive ornament with the anterior part of the valve covered with very small, regular puncta; area behind large sub-central tubercle comprising several deep, rectangular pits.

Weaver describes and illustrates *Curfsina deroo* from the Upper Cenomanian of Dorset (pl. 11, figs 1-4, p. 62). This is similar to the present material in shape but is smaller and differs in its ornament (reduced dorsal and median ribs; ornament less punctate, lacking the deep rectangular pits of *C. ceraunos).* The latter species also differs from *Curfsina? decorata decorata* Donze, 1972, from the French Cenomanian in its less pointed posterior and different ornament.

Published range. Pokorny recorded the species from the Turonian and Coniacian of Bohemia.

Range in this study. In the Trunch Borehole, this species ranges from the upper part of the Lower Campanian *Gonioteuthis quadrata* Zone (First Appearance SAG 449) into the Lower Maastrichtian *Porosphaera* Beds (Last Appearance SAG 213). It is most common in the Upper Campanian.

In the outcrop samples, the species occurs in the Coniacian *coranguinum* Zone (3) but is absent throughout the Santonian and Lower Campanian, reappearing in the Upper Campanian basal *mucronata* Chalk in two samples from Cringleford. It is sporadic in its occurrence, appearing in the lowest sample (SAG 93) of the Eaton Chalk at Eaton but is absent in the basal *mucronata* and Upper Weybourne Chalk at this locality. It is also present in the Middle Weybourne Chalk at Keswick, in the Beeston Chalk at Caistor St Edmunds and in the Paramoudra Chalk at Whitlingham. In the Lower Maastrichtian, the species occurs in the *O. lunata* Chalk and Grey Beds of Trimingham but was not encountered in either the pre-*Porosphaera* or *Porosphaera* Beds at Sidestrand.

Curfsina nuda (Jones & Hinde, 1890)

Pl. 18, figs 7-13.

1890 *Cythereis ornatissima* (Reuss) var. *nuda* Jones & Hinde, pl. 2, fig. 9,
non pl. 1, fig. 76; pl. 2, figs 12-14; pl. 4, fig. 14 (see remarks).

?1956 *Cythereis nuda* (Jones & Hinde). Deroo, p. 1519, pl. 4, figs 62-64.

1958 *Cythereis nuda* (Jones & Hinde). Howe & Laurencich, p. 216.

1964a *Cythereis nuda* (Jones & Hinde). Kaye, p. 67, pl. 7, figs 11, 13, 16.

1968 *"Cythereis" nuda* (Jones & Hinde). King, MS, pp 187-191, pl. 18, figs 5-7.

1978 *Curfsina nuda* (Jones & Hinde). Neale, p. 354, pl. 10, fig. 13, table 4.

Diagnosis. A medium species of *Curfsina* with a strong subcentral tubercle and well developed antero-ventral and postero-ventral spination. Anterior margin broadly rounded; dorsal and ventral margins straight and almost parallel, sloping to a narrow posterior. Lateral surface pitted

Dimensions.	L	H
LV male (MPK 11659)	0.66	0.35
LV female (MPK 11660)	0.61	0.37
RV male (MPK 11663)	0.64	0.33

Depository. MPK 11659 - 11665

Material. More than 400 specimens.

Remarks. The bulk of specimens attributed to *Cythereis ornatissima nuda* Jones and Hinde can be attributed to other species; the remaining specimen (fig. 9) is retained as the lectotype. Neale, 1978, illustrates this specimen (a left valve, catalogue number In 51685). Some of the specimens seen in the present study are smoother and less ornate than the lectotype, but the majority are identical to it. King, 1968, MS, illustrates specimens from the Lower Maastrichtian which are also identical to the lectotype and the present material.

Kaye, 1964a, notes that "additional material figured by Jones & Hinde (pl. 1, fig. 76; pl. 4, fig. 14) appears to be lost and cannot, therefore, be determined." Weaver, 1982 (p. 82, pl. 12, figs 3-6) erected a new species *Rehacythereis paranuda* from the British Upper Albian and Cenomanian and the Lower and Middle Cenomanian of northern France, incorporating Jones & Hinde's pl. 1, fig. 76 in this new species. Three further specimens of *C. ornatissima nuda* (Jones & Hinde, 1890, pl. 2, figs 12-14) were placed in synonymy with another new species *Planileberis scrobicularis* (Weaver, pl. 76, pl. 13-16). Wilkinson (1988a, MS, p. 412; pl. 21, fig. 9) illustrates a specimen of *Cythereis (Rehacythereis) paranuda* from the Late Albian, Early Cenomanian, Gault Beds and Cambridge Greensand of eastern England. This is identical to Weaver's type material.

King, 1968, MS (p. 191) notes that "Howe & Laurencich have pointed out that *Cythere quadridentata* Bosquet, 1854 is a junior homonym of *Cythere quadridentata* Baird, 1850, and as *Cythereis nuda* Jones & Hinde is a junior synonym of the former species, it must replace it as the valid name." This is not accepted by the present author, since the two species do not appear conspecific and the 1968 study is unpublished, and this thesis retains *Curfsina nuda* as a valid species, following Neale, 1978. King does, however, recognize that *C. nuda* "seems to belong to a distinct species group within the genus *Cythereis*" and notes that "to include these forms, Deroo is to erect a new genus, the type species of which will be *Cythereis major* Veen, 1936". This new genus was, of course, *Curfsina*. King notes that "in specimens from the *Gonioteuthis* Zone, the ornament is not so well developed and the small longitudinal riblet in the dorsal intercostal field is absent. This may be due to preservation or actual absence."

A few specimens resemble *Curfsina derooi*, described by Weaver, 1982, from the British upper Middle Cenomanian to the Upper Cenomanian (pl. 4, figs 1-4; full description of this species also reproduced in the Ellis & Messina Catalogue, book 56, suppl. 36 for 1990). Such specimens, however, do not show the reduced dorsal and median rib, In *C. derooi*, the median rib is almost non-existent, comprising only a sub-central tubercle and a second smaller tubercle towards the posterior margin. In *Curfsina nuda*, the median rib is clearly defined and appears to continue from the sub-central tubercle

and the valve is more elongate than the former species. The specimens in question have a weaker rib than typical specimens but are still recognizable as *C. nuda*.

The ornament on the lateral surface of *Curfsina nuda* is similar to that of *C. decorata decorata* Donze, 1972, from the French Cenomanian. The latter species is, however, larger with a more pointed posterior and a stronger dorsal rib. Another species, *C. subparva* Pokorny, 1969, from the Turonian of Bohemia, also has a similar ornament but, in this species, the antero-dorsal margin in the left valve is more rounded and the dorsal rib is more strongly developed.

Published stratigraphical range. King, 1968 MS, reports the species from the Lower Campanian *Gonioteuthis quadrata* Zone to the Lower Maastrichtian of Norfolk and notes that it is abundant in the Upper Campanian *mucronata* Zone. Neale, 1978, illustrates the lectotype from the ?Cenomanian detritus of Charing, Kent, noting (p. 354) that "the species ranges from Middle Albian to Maastrichtian, being particularly abundant in the Upper Campanian and lower Maastrichtian of eastern England."

Range in this study. *Curfsina nuda* is a common, long-ranging species in the Upper Chalk of Norfolk. Its range in the present study is Coniacian to Lower Maastrichtian, but it is more common in the Upper Campanian. In the Trunch Borehole, the species first appears in the lower part of the Lower Campanian *pilula* zone (FAD SAG 602, zone/subdivision 7) and ranges up into the Lower Maastrichtian *Porosphaera* Beds (SAG 213). A specimen assigned to *Curfsina* sp. cf. *C. nuda* was seen in a sample (SAG 637) from the Santonian *Marsupites testudinarius* Zone but this is not conspecific with the present material

In the outcrop samples, it ranges from the Coniacian basal *coranguinum* Zone (zone/subdivision 1) to the Lower Maastrichtian but is absent in the low *coranguinum* Zone (2). It appears again in the Coniacian *coranguinum* Zone (3) and the Santonian high *coranguinum* Zone (4) but was not seen in either the *Uintacrinus* Zone (5) or the *Marsupites testudinarius* Zone (6). It occurs in the Lower Campanian *pilula, pilula/quadrata* and *quadrata* zones (7-9), Upper Campanian basal *mucronata*, Eaton, Weybourne, Beeston and Paramoudra chalks (10-14) and in the Lower Maastrichtian pre-*Porosphaera* and *Porosphaera* beds of Sidestrand and the *O. lunata* and Grey Beds of Trimingham (15 to 18 respectively). The species was also present in the Santonian of Essex (SAG 2057, Witham Borehole; SAG 2058, Kelvedon Borehole) and in the Campanian flint-meal of Sonning, Berkshire.

Curfsina sp.

Pl. 17, fig. 21

Diagnosis. Subquadrate; anterior and posterior margins rounded; lateral surface with faint reticulation.

Dimensions.	L	H
LV (MPK 11652)	0.68	0.33

Depository. MPK 11652

Material. 2 specimens.

Remarks. Left in open nomenclature because of its rarity, this species cannot be assigned to any other species in the present study. It is a similar shape but is larger and lacks the characteristic pitting of either *Curfsina nuda* or *C. ceraunos* sp. nov. Its ornament is only faintly reticulate.

Range in this study. The species appears in the Upper Campanian Middle Weybourne Chalk (SAG 105) at Keswick, Norfolk and in the Paramoudra Chalk (SAG 79) at Crown Point Pit, Whitlingham.

Genus CYTHEREIS Jones, 1849.

Treatise reference. Q336

Treatise diagnosis. "Hinge paramphidont. Type species has ornament of low reticulations, but as currently understood, genus includes all reticulate, costate and spinose members of family with paramphidont hinge and simple muscle scar (4 vertically arranged adductor impressions, with V-shaped antennal scar in front). *L. Cret.-U. Cret.*"

Weaver, 1982, p. 63: "Valves large and strongly built. Hinge of left valve distinct, often bearing spines. Eye tubercle large; Longitudinal ribs often divided into spines or raised into frills. Muscle node large, often spinose or reticulate. Surface reticulate, pitted or smooth. Valves inflated in dorsal view."

Taxonomic note. The genus is discussed in detail in the note that follows.

A note on the genus *Cythereis*.

In 1849, Jones erected the genus *Cythereis* (pp 6-8) which is "rare among the recent ostracods but plentiful in the Cretaceous and Tertiary formations," as a sub-genus of *Cythere*. In *Cythereis*, Jones noticed that "a large external tubercle is always present on the central line on the anterior third of each valve, having a corresponding internal circular pit". In *Cythere (sensu stricto)*, the tubercle is not present but a "slight pit sometimes exists on the inner surface of the valves."

The early synonymy of *Cythereis* is as follows:

Cythere	Münster, 1830
Cytherina	Roemer, 1838
Cytherina	Roemer, 1840
Cytherina	Reuss, 1845
Cythere	Comuel, 1846
Cytherina	Williamson, 1847
Cypridina	Bosquet, 1847
Cythere (Cythereis)	Jones, 1849
Cythereis	Jones & Hinde, 1890.

Jones, 1849 (pp 14-15) gives a useful description of the characteristics of the subgenus and compares and contrasts *Cythereis* with *Cythere (sensu stricto)*. He states that "the hinges are formed of the same elements as in *Cythere* but the bars are scarcely distinct from the margins of the valve and the furrows are nearly obsolete; the hinge teeth are strongly developed. The hinge margin is proportionally longer and consists of the straight dorsal edge, extending from anterior to the posterior hinges, which respectively occupy the angle formed by the junction of the dorsal with the anterior borders. The other margins of contact have an arrangement very similar to that in *Cythere* proper, except that the flange of

the right and the groove of the left valve is generally more distinct and the ventral laminae more strongly developed" (Jones, 1849, p. 15).

In his 1849 Monograph, Jones reports nine species of *Cythereis* but only one of these can be classed as valid representatives of the genus; the other eight have been assigned to genera such as *Curfsina, Phacorhabdotus, Alatacythere, Protocythere, Veenia, Platycythereis, Amphicytherura, Mosaeleberis* and others. This is due to a more detailed understanding of taxonomy, following the work of such authors as Triebel, 1940; Sylvester-Bradley, 1948; Pokorny, 1963, and others, and a refinement in the criteria by which any one genus can be classified.

In their 1890 Monograph, Jones & Hinde report 12 species, of which only 4 can be retained within true *Cythereis,* the other species being assigned to such genera as *Veenia, Curfsina, Rehacythereis, Amphicytherura* and *Trachyleberidea* by subsequent authors. Kaye (1964a) extensively reviewed the species present in the Jones, Jones & Hinde, Chapman & Sherborn (1893) and Chapmans (1898) collections in the Natural History Museum, London. Table 2.3 shows this revision, brought up to date by the present author.

Sylvester-Bradley (1948, p. 793) notes that the genus had hitherto been placed in the family Cytherinae but differs fundamentally from Cythere and does not belong to the Cytheridae. The family Trachyleberididae, subfamily Trachyleberidinae, was erected to accommodate it and related forms.

The Trachyleberidinae consists of three related genera characteristic of Jurassic, Cretaceous and Tertiary-Recent intervals respectively. *Cythereis* differs from most Tertiary forms. Sylvester-Bradley (1948, p. 793) believes that these latter species should be "separated from *Cythereis* as a distinct genus for which *Trachyleberis* seems to be the prior name." The evolution of the hinge in this latter genus has proceeded further than in the former one. Middle Jurassic species showing an earlier stage of hinge evolution were accommodated within the new genus *Oligocythereis*. Van Morkhoven, 1963, illustrates the internal morphology and hinge structure of representatives of *Trachyleberis* (p. 176, figs 272, 273), *Cythereis* (p. 180, figs 277, 278) and *Oligocythereis* (p. 188, fig. 290; p. 189, fig. 291). If these are placed side-by-side, the differences in the structure of the hinge becomes clear. Damotte, 1965 (p. 238) discusses the nature and evolution of the hinge in certain trachyleberid genera, stating that some Campanian to Maastrichtian species (*Cythereis venusta, Cythereis senonensis)* are very close in hinge structure to certain Maastrichtian species of *Limburgina*. These two species were subsequently placed in the genus *Limburgina* Deroo, 1966.

If one looks through the synonymy of many Cretaceous *Cythereis* species, *Cythere*, as well as *Cythereis*, appears to have served as a "taxonomic dustbin" into which many different genera have been placed. An example may be seen in the case of *Cythere (Cythereis) lonsdaleiana* of Jones, 1849. In 1890, the generic name was altered to *Cythereis* (Jones & Hinde, retained by Bonnema, 1941; Kaye, 1964a, and others). Later workers reassign the species to *Phacorhabdotus* (e. g. Herrig, 1966; Damotte, 1971a, this study). Another species *Cythereis macropthalma* (Veen, 1936; Howe & Laurencich, 1958) was originally designated *Cypridina macropthalma* Bosquet, 1847. Later workers, from Damotte, 1971a to the present assign the species to *Mosaeleberis*. The synonymy of *Curfsina nuda* Jones & Hinde begins with the original name: *Cythere (Cythereis) lonsdaleiana*, not to be confused with *Cythereis*

lonsdaleiana (= Phacorhabdotus lonsdaleiana) of the same author. The synonymy also includes five or six different species (see Kaye, 1964a, p. 67, for a detailed explanation and full synonymy). Deroo, 1956, designated the species as *Cythereis nuda,* but it is now assigned to *Curfsina.*

The early use of *Cythere* is, however, valid for certain species retained within *Cythereis. C. ornatissima* (Reuss), and illustrated by Kaye (1964a, p. 64) from the Upper Chalk of Norwich, is a problematic species; large numbers of different forms have been assigned to it in the past. In synonymy, generic classification alters from *Cytherina ornatissima* in Reuss' original type description (1846), to *Cythere* (1874), eventually changing to *Cythereis.* Pokorny extensively revised the species in 1963 (see also Kaye, 1964a, for a full discussion).

It quickly becomes obvious, to anyone working through the literature, that the genus *Cythereis (sensu lato)* has been used to accommodate a large number of Cretaceous species of very different size, shape and morphology. All the species in the British Upper Cretaceous show a wide ornamental variability. Kaye, 1964a, writes that a thorough investigation of large numbers of specimens to determine the variability of any one species is needed in most cases on the scale of Pokorny's 1963 revision of *Cythereis ornatissima.*

Triebel (1940) described true representatives of the genus with a paramphidont hinge. In 1948, Sylvester-Bradley restricted *Cythereis* to the Cretaceous; this is the convention followed by most ostracod workers.

Gründel, 1973, divided it into *Cythereis (s. s.)* and new genera *Veeniacythereis, Parvacythereis, Rehacythereis* and *Cornicythereis.* Damotte (1977) regards *Cornicythereis* as a sub-genus of *Cythereis* and *Rehacythereis* a junior synonym, because of the close affinity between species. Other authors (Weaver, 1982; Witte *et al.,* 1992) consider them separate: *Cornicythereis* being distinguished by its inflated longitudinal ribs and lack of other surface ornamentation. *Rehacythereis* can be more difficult to distinguish. It was originally separated from *Cythereis* by its continuous dorsal and ventral ribs and non-spinose sub-central tubercle (Gründel, 1973; Majoran, 1989, p. 19). Gründel, 1974, considered *Cythereis* to be an Albian descendant of *Rehacythereis,* from which it evolved towards its "hallmark features I. e. interrupted dorsal and ventral ridges and a generally tuberculate or reticulate sub-central tubercle." Babinot, 1980 (p. 123), considers this evolution as possibly representing a general trend among Albian to Cenomanian forms. Gründel also considered *Rehacythereis* to be a possible ancestor of *Trachyleberidea* but other authors (Liebau, 1975, p. 363) express doubts. The current author agrees; intergeneric relationships are, at best, tentative. In the present study, both *Cythereis* and *Trachyleberidea* are well represented. It is clear that the one could not have given rise to the other.

Damotte, 1977, raised doubts over *Rehacythereis,* considering it a sub-genus of *Cythereis* (Damotte, 1971a, p. 52). Majoran (1989, p. 20) found intermediates between the two genera and suppressed the former to "avoid the arbitrary assignments of intermediates." In the present material, however, there are no intermediate forms and the two genera can be consistently separated. Majoran also illustrates specimens doubtfully referred to *Curfsina.* Since representatives of this genus usually have eye tubercles and an anteromarginal rib; features not evident in the specimens in question, it is likely they are not *Curfsina.* Gründel, 1973; Damotte & Rey, 1980, place such forms in *Rehacythereis.*

Table 2.3 - A revision of the forms assigned to *Cythereis* by Jones (1849), Jones & Hinde (1890), Chapman & Sherborn (1993) and Chapman (1898). This follows Kaye's (1964a) revision, updated by the present author

Jones, 1849

species name	Kaye's revision	current author and others
Cythereis triplicata (Roemer)	*Protocythere lineata*	as Kaye, 1964a
Cythereis quadrilaterata (Roemer)	*Cythereis folkstonensis*	*Cornicythereis larivourensis* (Damotte & Grosdidier) Weaver, 1982, p. 61
Cythereis ciliata (Reuss)	*Cythereis thorenensis*	*Cythereis hirsuta* (see Weaver, 1982 p. 64), *Cythereis thoerenensis* Weaver, 1982, p. 68
Cythereis lonsdaleianus Jones	*Cythereis lonsdaleianus* (Jones)	*Phacorhabdotus lonsdaleianus*
Cythereis cornuta (Roemer)	*Cythereis nuda*	*Curfsina nuda*
Cythereis alata (Bosquet)	*Alatacythere robusta* (Jones & Hinde)	*Alatacythere robusta* (Jones & Hinde)
Cythereis interrupta (Bosquet)	*Veenia harrisiana* (Jones)	*Mandocythere harrisiana* (see Weaver, 1982, p. 52)
Cythereis gaultina (Jones)	*Platycythereis gaultina* (Jones) (see also Mertens, 1956, p. 209	*Platycythereis gaultina*
Cythereis macropthalma (Bosquet)	*Amphicytherura chelodon* (Marsson)	Kaye's figured specimen does not conform to *Amphicytherura*. The current author would assign it to the genus *Mosaeleberis*

Table 2.3 (continued)

1890 Jones & Hinde

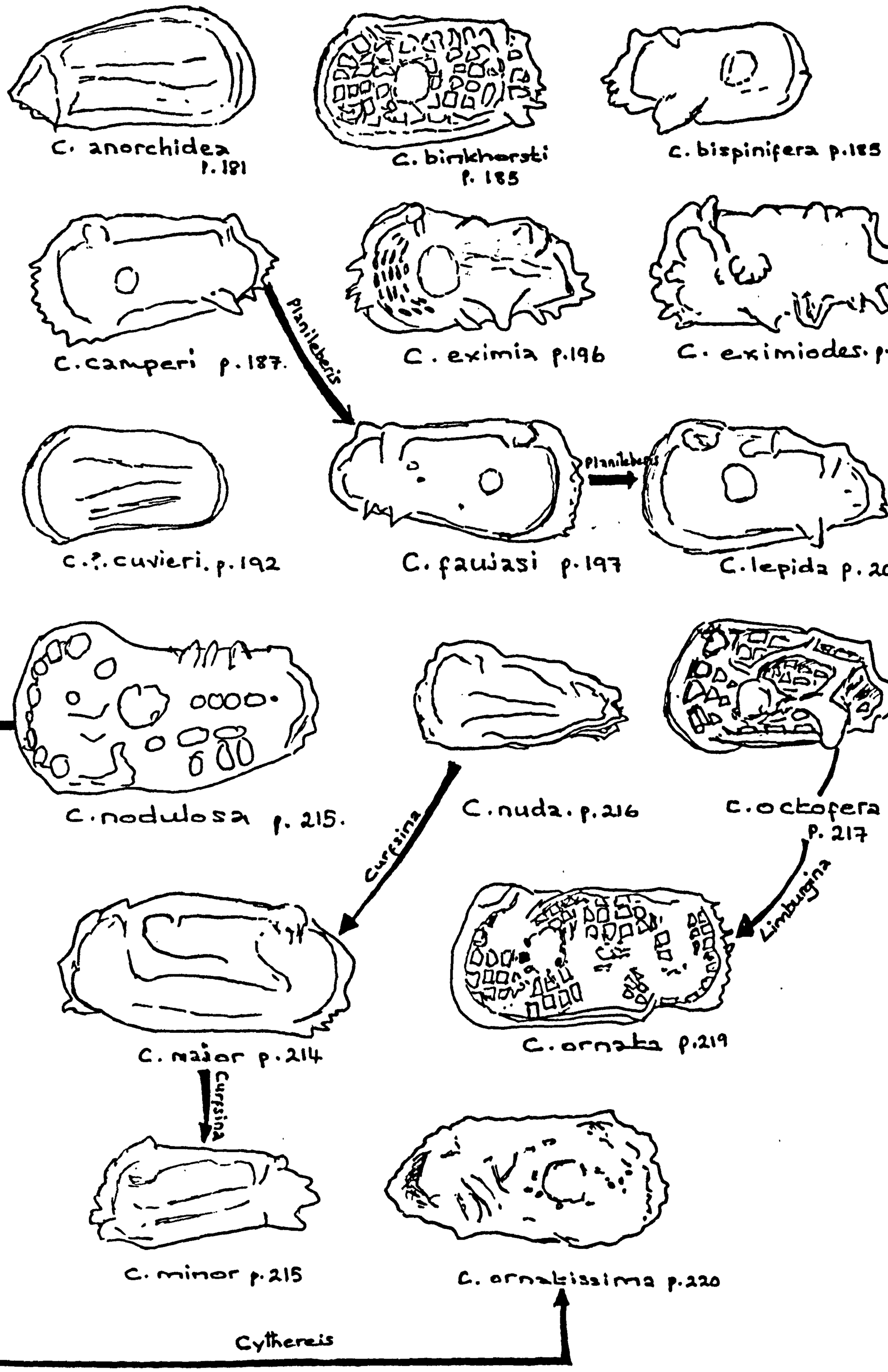
species name	Kaye's revision	current author and others
Cythereis auriculata (Cornuel)	*Veenia harrisiana* (Jones)	Damotte, 1971a (p. 61) assigned *Cythere auriculata simplex* of Cornuel to *Cythereis simplex*. The present author would agree. The specimens of Jones & Hinde, as well as those of Kaye, 1964a, appear to be more like *Cythereis*
Cythereis ornatissima paupera	no material (see Kaye, 1964a, p.66)	?
Cythereis ornatissima nuda	in part *Cythereis nuda*	specimens referred to *Cythereis nuda* by Kaye belong to *Curfsina*, but see Weaver, 1982, p. 76
Cythereis ornatissima reticulata	*Cythereis reticulata* (Kaye, 1964, Damotte, 1971a)	*Cythereis reticulata*
Cythereis ornatissima radiata	*? Cythereis thoroensis* (see Kaye, 1964a, p. 66)	?
Cythereis ornatissima stricta	*Cythereis lurmannae* Triebel	The current author follows Weaver, 1982, and others in assigning the species to *Rehacythereis, since C. lurmannae* is the type species for this genus.
Cythereis wrightii	*Cythereis wrightii*	*Cythereis wrightii*
Cythereis tuberosa	no material found by Kaye, 1964a	discussed later in this chapter
Cythereis icenica	*Amphicytherura chelodon*	*Amphicytherura chelodon*
Cythereis icenica quadrata	no material found by Kaye, 1964a	?
Cythereis vallata	no material found by Kaye, 1964a	discussed later in this chapter
Cythereis spinicaudata	*Trachyleberidea acutiloba*	*Trachyleberidea acutiloba*

Table 2.3: (continued)

1893 Chapman & Sherborn

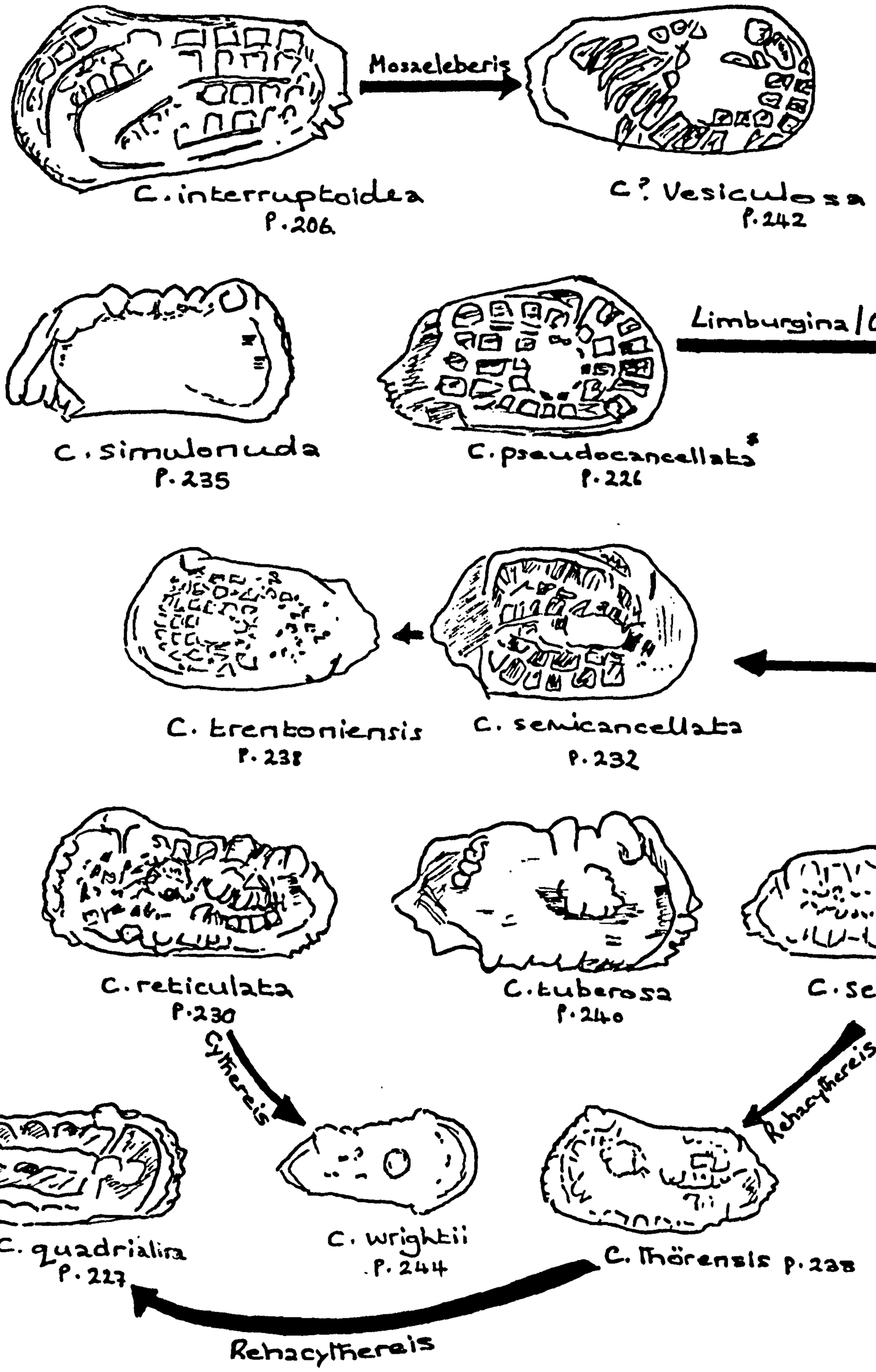
species name	Kaye's revision	current author and others
Cythereis triplicata lineata	*Protocythere lineata* (Chapman & Sherborn.	*Protocythere lineata*
Cythereis rudispinata Chapman & Sherborn	*Protocythere rudispinata*	*Protocythere rudispinata*
Cythereis rudispinata of Triebel, 1940	*Cythereis corrigenda* (see Kaye, p. 62)	Damotte, 1971a, included *C. corrigenda* of Kaye in *Cythereis matronae*. The present author would assign the species to *Matronella*, following Weaver, 1982; Symmonds 1996, MS and other recent authors.
Cythereis wrightii aculeata	*Cythereis reticulata*	Kaye, 1964a, retained *C. wrightii* within *Cythereis* and reassigned the subform to *C. reticulata*. The present author is in agreement.
Cythereis excavata	*Platycythereis excavata* (see Kaye, 1964a, p. 67)	Main species: *Platycythereis gaultina*, subspecies = *P. chapmani* of Kaye 1964a (see also Weaver, 1982).

Figure 2.4. A selection of some of the forms assigned to *Cythereis* by Howe & Laurencich, 1958.



→ join species which have been reassigned to the same genus.

Figure 2.4 (continued). A selection of some of the forms assigned to *Cythereis* by Howe & Laurencich



* should be C. pseudosemicancellata

→ join species which have been reassigned to the same genus

Pokorny & Colin, 1978, discuss parallelism in the phylogeny of the Protocytheridae and the Trachyleberidae, especially in the new genus *Kamajcythereis* based on the type species *Cythereis kamajcensis*. Pokorny (1964, p. 283) erected *Spinocythereis* (spine + *Cythereis)* to accommodate forms that differ from *Cythereis* by their "small size, laterally much compressed, without pronounced hinge ears in the left valve. Riblets of reticulation bear numerous variously orientated small spines that partially fill the meshes of reticulation. The sculpture of the larval stage is much more similar to that of adults, whereas in *Cythereis,* it is much weaker than in adult specimens." Pokorny also notes the genus resembles *Platycythereis* in the lack of a hinge ear, the flattened carapace and complicated pattern of reticulation. The two, however, belong to different phylogenetic lineages. The "spongeous" sculpture in the latter developed before the oldest known representative of *Spinicythereis*. Large marginal spines are present in the former genus but absent in the latter. The hinge teeth of *Platycythereis* are "of a more primitive type" than those of the latter genus. It should be noted that Pokorny's genus was erected on the type species *Cythere geinitzi* Reuss, 1874. This is also the type for *Trachyleberidea*, which has 9 years seniority (Bowen, 1953). It is likely that *Spinicythereis* is a junior synonym of *Trachyleberidea*. In a search through more than 1000 papers, the present author found little reference to Pokorny's genus.

Cythereis campaniensis sp. nov.

Pl. 18, figs 14-21.

Derivatio nominis: Named for its occurrence in the Upper Campanian of Norfolk.

Holotype. Female left valve (MPK 11668)

Type level. Upper Campanian Beeston Chalk.

Type locality. Caistor St Edmunds, Norfolk.

Diagnosis. An elongate species with a very well-developed paramphidont hinge; anterior margin with broad denticulate rib. Sub-central tubercle large with 2-3 small tubercles. Median rib in LV short, straight, absent in RV or obscured by ornament. Posterior narrow, smooth with small posteroventral spine.

Description. Large, elongate; greatest height at approximately mid-point; anterior margin rounded; apex at mid-point, with a broad, strongly defined anterior rib with 7-8 small denticles; a faint second narrow rib runs parallel to anterior margin; intercostal areas between two ribs smooth. Eye tubercle large, hemispherical, with a clear hinge ear and a small, short curving rib running from the eye tubercle halfway to large sub-central tubercle, which is spherical and boss-like with 2-3 small rounded tubercles. Dorsal rib weak; dorsal margin straight and slightly spinose, sloping down to posterior; ventral margin partially or fully obscured by straight ventral rib. Posterior narrow, drawn-out with small postero-ventral spine, smooth with faint, narrow rib, apex below mid-point; Median rib short, straight; in male RV sometimes obscured by ornament, occurs just after sub-central tubercle but is not connected. Ornament regularly reticulate. Clear sexual dimorphism; males narrower and more elongate than females, females less elongate and more inflated. Ontogeny unknown.

Marginal zone moderately broad, widest anteriorly. Hinge well-developed- Paramphidont. In RV consisting of a high pentalobate anterior tooth and a deep, rounded socket; hinge line straight with no accommodation groove - median element and a high pentalobate posterior tooth; LV complementary. Other internal features not seen.

Dimensions.	L	H
Holotype, female LV (MPK 11668)	0.80	0.43
Paratype, female LV (MPK 11666)	0.80	0.43
Paratype, male LV (MPK 11667)	0.85	0.40
Paratype, female RV (MPK 11673)	0.81	0.43
Paratype, male RV (MPK 11670)	0.81	0.42
Paratype, juvenile LV (SAG 81)	0.73	0.34

Depository. MPK 11666 to 11673

Material. At least 12 specimens.

Remarks. This species is similar in shape and ornament to *Cythereis agedincumensis* Damotte (1964, p. 320) from the Upper Campanian of the Paris Basin, also recorded from the Lower Campanian (Damotte, 1965b, 1971a, p. 75). The latter first appears in the Upper Santonian and sporadically into the basal Upper Campanian and is smaller than the present species (males 0.74-0.76mm, females 0.71-0.73mm; *C. campaniensis* males 0.85mm, females 0.80mm). However, Damotte's figured specimens do not look like those illustrated as *Mauritsina agedincumensis* by Babinot *et al.*, 1985. The ornament in the later illustrated specimens is more similar to the present material but the sub-central tubercle in *C. campaniensis* sp. nov. is larger, more prominent and spinose; anterior rib thicker, broader and more strongly defined, with more prominent marginal denticles. The hinge in the present species is more strongly paramphidont; high pentalobate anterior tooth and a deep, rounded socket, high pentalobate posterior tooth; LV complementary.

The present species has a finer ornament than *Cythereis hirsuta* Damotte & Grosdidier, or *C. reticulata* Jones & Hinde, illustrated by Witte *et al.*, 1992 (pl. 6, figs 1-3, fig. 7). Both are broader and less elongate. Kaye, 1964a, illustrates the latter from Jones & Hinde's type material (pl. 8, figs 16-19, p. 67), showing more heavily calcified valves which are strongly inflated in dorsal view, with a double row of anterior spines or tubercles and 6 short postero-ventral spines. The ventral rib is more spinose and the eye tubercle larger than the present species. *C. campaniensis* sp. nov. is similar to *Cythereis neumannae* Colin, 1974 (pl. 2, figs 1-2) from the French Upper Cenomanian, in shape and general ornament. The latter species differs, however, in its lack of ornament in the anterior part of the valve in front of the sub-central tubercle, which is smaller than in the former species. The median rib is obscured in the right valve by ornament, but Colin does not illustrate a LV; the anterior rib is also slightly narrower and less pronounced, the dorsal margin is less straight. *C. neumannae* is also larger (0.93-1.10mm; present species ranges from 0.80 to 0.85mm in length).

Range in this study. This species is absent in the Trunch Borehole and rare in the outcrop samples, restricted to the Upper Campanian (Beeston and Paramoudra Chalks) at several localities.

Cythereis cf. *C. coronata* Weaver, 1982

Pl. 18, fig. 22, 23; pl. 19, figs 1-2

cf. 1982 *Cythereis coronata* Weaver, p. 63, pl. 12, figs 15-19; pl. 13, fig. 1.

Diagnosis. A large heavily calcified, sub-rectangular species, characterized by crown-like large subcentral tubercle with five nodes; hinge ear non- spinose.

Dimensions.	L	H
RV female (MPK 11672)	0.80	0.42
LV male (MPK 11673)	0.85	0.37
LV male (MPK 11674)	0.85	0.38
RV female (MPK 11675)	0.81	0.42

Depository. MPK 11672 - 11675

Material. At least 20 specimens.

Remarks. *Cythereis coronata* Weaver, 1982, and *C.* cf. *C. coronata* of this study are similar to *Cythereis ornatissima icenica* subsp. nov., but in these two forms, the double row of small tubercles is more distinct. The latter species differs in its more inflated valves, lack of a distinct anterior marginal rim and different marginal rib composition. It is slightly larger; its dorsal margin is straight and slopes less towards the posterior. The ornament is different; a series of round tubercles and smooth intercostal areas compared to a reticulate network behind the sub-central tubercle. The present material is smaller than that of Weaver and differs in its stratigraphical age; specimens are not quite as heavily calcified. Specimens do, however, show the crown-like subcentral tubercle diagnostic in Weaver's material.

Published range. Weaver reported the species from the top of the Lower Cenomanian of Southerham, Sussex and in the Middle Cenomanian of Bluebell Hill, Kent.

Range in this study. In the outcrop samples, this species first appears in the *Gonioteuthis quadrata* Zone (9) of the Lower Campanian and occurs throughout the Upper Campanian (basal *mucronata,* Eaton, Weybourne, Beeston and Paramoudra Chalks; 10-14) at different localities across Norfolk. In the Lower Maastrichtian, it occurs in the pre-*Porosphaera* Beds of Sidestrand and in the *O. lunata* Chalk and Grey Beds of Trimingham (zone/subdivisions 15, 17, 18).

Cythereis cf. *C. hirsuta* Damotte & Grosdidier, 1963

Pl. 19, fig. 3

cf. 1963 *Cythereis hirsuta* Damotte & Grosdidier, p. 56, pl. 2, figs 5 a-g.

Diagnosis. A large, reticulate, sub-rectangular species with a clear hinge ear; anterior margin broadly rounded with broad denticulate marginal rim. Dorsal and ventral margins straight and spinose; ventral rib reduced to series of tubercles; sub-central tubercle prominent, not connected to short, straight median rib. Posterior narrow and drawn-out.

Dimensions.	L	H
LV (MPK 11676)	0.90	0.48

Depository. MPK 11676

Material. 2 specimens

Remarks. The present material is smaller than Damotte & Grosdidier's *C. hirsuta* but can be compared to it. The reticulate ornament is less strongly developed and slightly more open. It is smaller than material figured by Kaye (1964a, p. 68, pl. 1, figs 14-15, 17); Gründel (1964, pl. 1, fig. 6, 7; 1966, pl. 6, figs 16, 20), Damotte (1971a, pl. 2, fig. 11), Weaver, 1982 (pl. 12, figs 7-11) or Wilkinson, 1988a MS (pl. 20, figs 1-2) and also shows a different stratigraphical occurrence. Weaver discusses this species in more detail (p. 65), as does Wilkinson (pp 400-401).

Published range. Middle Albian to Middle Cenomanian of Great Britain, France and Germany.

Range in this study. In the Trunch Borehole, this species was found in a single sample from the Lower Campanian *G. quadrata* Zone (SAG 462). In the outcrop samples, it is restricted to the Upper Campanian Eaton Chalk at Eaton, Norfolk.

Cythereis cf. *C. longaeva longaeva* Pokorny, 1963

Pl. 19, figs 4-7

cf. 1963 *Cythereis longaeva longaeva* Pokorny, p. 27, pl. 2, fig. 2; pl. 5, figs 1, 3, 4; pl. 7, figs 5-7.

cf. 1968 *Cythereis (Cythereis) longaeva* Pokorny. King, MS, pl. 11, figs 6-8.

cf. 1968 *Cythereis (Cythereis) cf. longaeva* Pokorny. King, MS, pl. 11, fig. 9; pl. 12, figs 1-2.

cf. 1970 *Cythereis longaeva longaeva* Pokorny. Gründel, pl. 1, figs 9-10.

Diagnosis. See Pokorny, 1963, p. 27, for detailed description (also King, 1968, MS).

Dimensions.	L	H
LV female (MPK 11677)	0.80	0.41
LV male (MPK 11678)	0.85	0.37
LV male (MPK 11679)	0.85	0.37

Depository. MPK 11677-11679, 11835

Material. 5 specimens.

Remarks. King, MS, writing on Upper Campanian forms assigned to *Cythereis* cf. *longaeva* (here considered synonymous with *C. longaeva longaeva)* notes that "the examination of more material will probably permit the erection of a new species for these forms." His specimens do, however, closely resemble those of the present study and they are included in the above synonymy. The present material is close to Pokorny's original description differing in its smaller size; it is also less heavily calcified and the sub-central tubercle is more spinose and the reticulate ornament less well developed.

Published range. Pokorny first recorded the species from the Middle to Upper Turonian of Czechoslovakia. King, 1968 MS, records *Cythereis longaeva* from the *Marsupites* Zone (Santonian) and the lower part of the Upper Campanian and *C. cf. longaeva* from the Upper Campanian of Norfolk and Northern Ireland. Gründel, 1970, records the species from the Lower to Middle Turonian of Saxony, while Damotte, 1971a (pl. 3, fig. 8) notes its occurrence in the Turonian to Coniacian of the Paris Basin. Babinot *et al.,* 1981, record the species from the Coniacian of Germany.

Range in this study. The species occurs in the Coniacian *coranguinum* Zone at South Pickenham (SAG 113) and in the Lower Maastrichtian Grey Beds at Trimingham (SAG 2007).

Cythereis ornatissima (Reuss) *icenica* subsp. nov.

Pl. 19, figs 8-13.

Derivatio nominis: "*Icenica*" refers to the occurrence of this subspecies in Norfolk, after the Iceni -the Celtic tribe in the area during the Iron Age.

Holotype. Female RV (MPK 11681)

Type level. SAG 2007, Lower Maastrichtian Grey Beds.

Type locality. Trimingham, Norfolk.

Diagnosis. A large subspecies of *C. ornatissima* characterized by its smooth anterior marginal area anterior of the sub-central tubercle with only a very faint row of indistinct tubercles; the sub-central tubercle spinose, with a ring of five nodes; ventral rib reduced to a series of rounded tubercles; a second row of four postero-ventral tubercles below the first.

Description. Large. Rather inflated. Heavily calcified and sub-rectangular in lateral view; sub-quadrate in dorsal view of the complete carapace, double row of short, regularly spaced spines along the dorsal margin. Postero-ventral spine especially prominent; maximum width occurs just below this. Maximum height at anterior cardinal angle; maximum width through sub-central tubercle; eye tubercle small but distinct; hemispherical - spherical. Some specimens with a short rib extending down from the eye tubercle in LV; this is absent in the RV. Anterior margin broadly rounded, spinose with a tuberculate anterior rib; anterior area in front of sub-central tubercle smooth apart from a ventral double row of faint tubercles, fi ve in each row. Sub-central tubercle prominent, spinose with a ring of 5-6 very small nodes; dorsal and ventral margins straight, gradually sloping to posterior; dorsal margin spinose, 6 short spines and a larger postero-dorsal spine. In the RV, there are a further 2 spines, in the LV, there is a second spine behind the postero-dorsal one. Dorsal rib absent or reduced; posterior margin narrow and acute, postero-dorsal slope with 2 short spines; postero-ventral slope more spinose with a clear rib bearing a further 4 spines. Ventral margin straight, weakly spinose; ventral rib reduced to 7-8 spines; in posterior of valve, a second row of four spines almost touches the upper row. Below the postero-dorsal spine, on a straight line across the valve, is a postero-ventral spine of equal size. Ornament restricted to posterior, consisting of rounded tubercles or short spines; median rib reduced to two larger tubercles at mid-point between postero-dorsal and postero-ventral spines. Sexual dimorphism not marked. LV anterior margin slightly broader than in RV, posterior more narrowly rounded, less acute.

Inner margin narrow, slightly broader at posterior ; line of concrescence coincident with inner lamella; marginal pore canals not seen. Muscle scars obscured or indistinct. Hinge in RV - small crenulate anterior tooth, smooth-weakly crenulate median element; posterior tooth crenulate and only weakly pentalobate.

Dimensions.	L	H
Holotype, female RV (MPK 11681)	0.90	0.49
Paratype, female RV (MPK 11680)	0.85	0.43
Paratype, female LV (MPK 11682)	0.88	0.48
Paratype, male RV (MPK 11683)	0.85	0.44
Paratype, C (MPK 11685)	0.86	0.47
Paratype, RV A-1 juv. (MPK 11684)	0.78	0.35

Depository. MPK 11680-11685.

Material. 20 specimens.

Remarks. King, 1968 MS, erects a new genus - *Herrigella* based on the type species *Cythereis zygopleura* Pokorny, 1965. This designation can be ignored, however, since King's work is unpublished and all forms assigned to *Cythereis (Herrigella)* clearly conform to true-*Cythereis*.

The present material differs sufficiently from *Cythereis ornatissima ornatissima* Reuss, 1846, to be considered a new subspecies. *C. ornatissima* as figured by Neale, 1978 (p. 366, pl. 17, figs 10-12) ranges from the Campanian to Lower Maastrichtian in British records, but is significantly larger than the material seen in the present study (0.99-1.08mm in length; present material 0.85-0.90mm), with a more spinose anterior margin. The anterior marginal area in front of the sub-central tubercle in the present specimens is smooth with a double row of faint tubercle, while in the nominative subspecies, in the RV, these tubercles are larger and more distinct. The subspecies of Pokorny (1963) are all larger and more ornate; Kaye (1964a) extensively revised *Cythereis ornatissima* but neither describes nor illustrates anything similar to the present subspecies (see Kaye, 1963, pp 64-66; pl. 8, figs 1, 2, 4, 6).

Cythereis coronata Weaver, 1982, and *C.* sp. cf. *C. coronata* of this study are similar to the present subspecies, but in both, the double row of small tubercles is more distinct. *C. ornatissima icenica* differs in its more inflated valves, lack of a distinct anterior marginal rim and different marginal rib composition. The latter is also slightly larger; its dorsal margin is straight and slopes less towards the posterior. The ornament is also different; a series of round tubercles and smooth intercostal areas compared to a reticulate network behind the sub-central tubercle.

The material of the present study is smaller and more spinose than *C. folkstonensis* Kaye, 1964a (p. 63, pl. 7, figs 1-5) from the ?Albian of Kent. Both show reduction of the ventral ribs (6-7 in the former, 9 in the latter), but the former lacks the median row of 6 tubercles behind the sub-central tubercle. Kaye (p. 63) notes that this is "the most diagnostic feature of *C. folkstonensis.*" The sub-central tubercle is more spinose in the present material, consisting of a ring of 5-6 rounded nodes; Kaye's specimens have a smooth to weakly spinose rounded tubercle, with a clear longitudinal row of tubercles along the reduced dorsal rib, a distinct anterior marginal rib and a larger eye tubercle. The present material is similar in shape in lateral view and in dorsal and ventral views to *Cythereis peturbatrix* Pokorny, 1965, illustrated by Gründel, 1970 (pl. 2, figs 2-4) but this species differs in its smaller size and the presence of a clear anterior rib. Gründel reported a size range of 0. 64-0. 66mm (females), 0. 68-0. 76mm (males); the present material is 0. 85-0. 90mm in length, with the posterior apex at or just below mid-height; in *C. peturbatrix,* it is well below mid-height.

Range in this study. In the outcrop samples, this subspecies is restricted to the Lower Maastrichtian pre-*Porosphaera* Beds of Sidestrand and the Grey Beds of Trimingham (Zone/subdivision 15 and 18).

Cythereis zygopleura Pokorny *varia* Herrig, 1965

Pl. 19, figs 15, 17-19; pl. 20, figs 1-17.

1965 *Cythereis zygopleura varia* Herrig, pp 403-419, pl. 1; pl. 2, figs 1-4; pl. 3, figs 1-2.

1966 *Cythereis zygopleura varia* Herrig, pp. 810-823, text figs 69-73; table 26, pl. 22, figs 1-3, 6, 7.

1967 *Cythereis zygopleura varia* Herrig, pl. 1, figs 1-6, 10-11.

1968 *Cythereis (Herrigella) rowei* King, MS, pl. 14, figs 6-8.

Diagnosis. A subspecies of *Cythereis zygopleura* with a variable ornament ranging from strongly reticulate centrally and reticulo-punctate and then punctate peripherally, to specimens with well developed conjunctive spines or tubercles or specimens with a reduced or smooth ornament. Anterior margin dentate, broadly rounded with a clear marginal rib; posterior margin narrow and elongate. Sub-central tubercle large, prominent and spherical with at least two spines. It is separate from the distinct median rib. Herrig, 1967, describes the various "form-types" in detail; the distinctions between these will not be repeated here.

Dimensions.	L	H
RV (MPK 11695)	0.86	0.48
LV (MPK 11701)	0.86	0.48
RV (MPK 11697)	0.83	0.43
RV (MPK 11693)	0.84	0.45

Depository. MPK 11691-11709 (*C. zygopleura varia)*; MPK 11689-11690 (transitional forms), MPK 11836

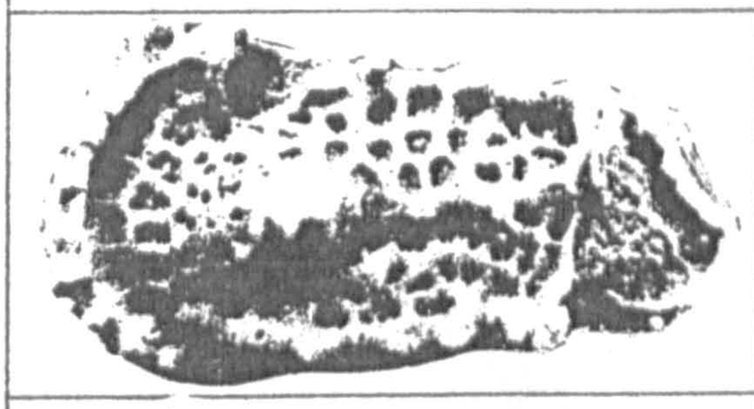
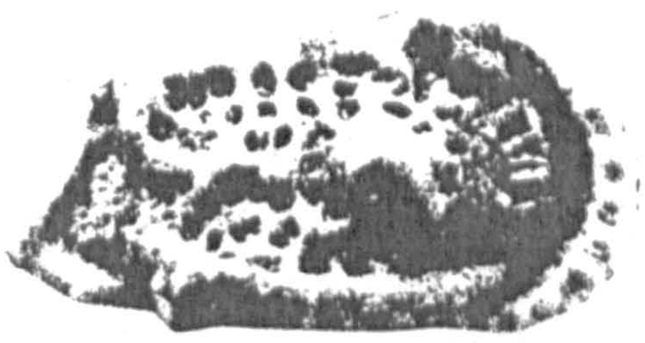
Material. More than 150 specimens.

Remarks. *Cythereis zygopleura expressa,* recorded by Herrig (1967, pl. 2, figs 1-2) from the Upper Campanian of Northeastern Germany, is a larger, more strongly reticulate species than either *C. zygopleura zygopleura* or *C. zygopleura varia.* It was not seen in the present study.

C. zygopleura varia is an extremely variable species in its ornament but valves are commonly punctate in front of the large subcentral tubercle and reticulate behind it. *C. zygopleura zygopleura* shows no antero-lateral puncta. The reticulation in this subspecies covers the entire lateral surface of the valve (see Herrig, 1967, pl. 1, fig. 9). In transitional forms (1967, pl. 1, fig. 7; this study, Pl. 20, figs 12, 15), some puncta are present anterior of the subcentral tubercle. Herrig, 1967, notes that in Northeastern Germany, *C. zygopleura zygopleura* passes through a transitional stage in the Lower Campanian (also noted by King, 1968, MS, p. 175) into *C. zygopleura varia* in the Upper Campanian. The latter species is discussed extensively, with length-height measurements for the different morphological variants or "form-types".

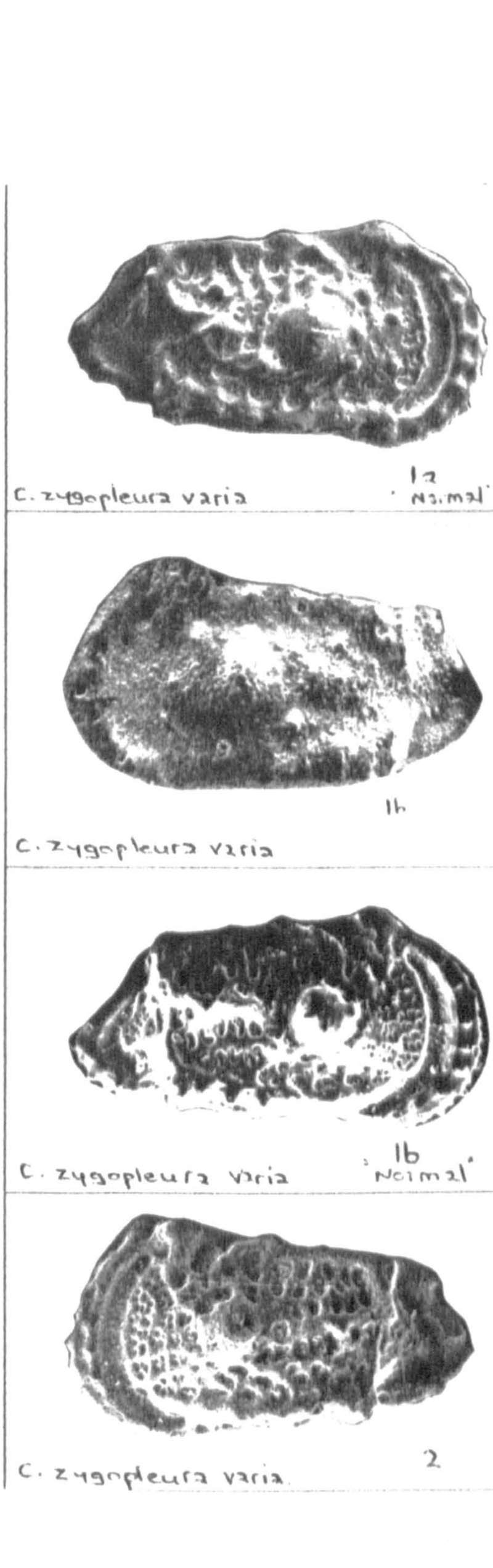
The stratigraphical ranges of the various subforms in Herrig's study are presented in table 2.4. Similar ranges are also seen (table 2.5a and 2.5b) in the Upper Chalk of East Anglia.

Table 2.4- Range of *Cythereis zygopleura zygopleura* and *C. zygopleura varia* according to Herrig, 1967- illustrated specimens copied from this publication (plate 1, figs 1-7)

	Co	S	LC	UC	LM	
						HERRIG 1967 PLATE 1, Fig. 7.
						Fig. 8,
						Fig. 6,
						Fig. 5.
						Figure 3,
						Figure 2,
						Figure 1,

7 – *C. zygopleura zygopleura* "normalform", 8- *C. zygopleura zygopleura* "transitional", 6- *C. zygopleura varia* form 1a, 5- *C. zygopleura varia* form 1a "normalform", 3- C. zygopleura varia form 1b "normalform", 2- *C. zygopleura varia* form 1b – reduced sculpture, 1- *C. zygopleura varia* form 2 "normalform"

Table 2.5a. Range of *Cythereis zygopleura varia* in the Trunch Borehole.



LC		UC				LM
O. pilula	G. quadrata	B. mucronata zone				B. lanceolata zone
		WC	CSB	BC	PC	Sidestrand Chalk

WC - Weybourne Chalk, CSB - Catton Sponge Beds, BC - Beeston Chalk, PC- Paramoudra Chalk

Table 2.5b.Range of Cythereis zygopleura zygopleura and C. zygopleura varia in the the Upper Cretaceous of East Anglia (Outcrop samples)

Co Sa			LC		UC					LM
			O. pilula	*G. quadrata*	B. mucronata zona					*B. lanceolata zone*
					WC	EC	CSB	BC	PC	Sidestrand Chalk
C. zygopleura zygopleura **8**										
C. zygopleura zygopleura **(transitional 7**										
C. zygopleura varia **1a "normalform" 6**										
C. zygopleura varia **1a "fehlender Feinskulpture 5**										
C. zygopleura varia **1b "normalform" 4**										
C. zygopleura varia **1b "reduced ornament" 3**										
C. zygopleura varia **2 – poorly reticulate 2**										
C. zygopleura varia **2 "normalform" 1**										

WC = Weybourne; EC Eaton Chalk CSB = Catton Sponge Beds; BC = Beeston Chalk; PC = Paramoudra Chalk

Standard abbreviations are used to denote Coniacian (Co), Santonian (Sa); Lower Campanian (LC); Upper Campanian (UC) and Lower Maastrichtian (LM) intervals

Published range. Herrig, 1966, described the species from the Campanian and Lower Maastrichtian of Northeastern Germany. Form 1a ("normalform") is present in the Upper Campanian. In the uppermost Upper Campanian, form 1b is recorded, giving way to form 2 in the Lower Maastrichtian. King, 1968, MS, includes *C. zygopleura varia* in synonymy with a new species *Cythereis (Herrigella) rowei*, which occurs in Norfolk in the Upper Campanian Weybourne Chalk up into the Lower Maastrichtian Sidestrand Sponge Beds. In the opinion of the present author, however, King's unpublished species should be regarded as a junior synonym. They are probably just smooth morphotypes of this variable species.
Range in this study.In the Trunch Borehole, the species ranges from the Upper Campanian to the Lower Maastrichtian with forms transitional between *C. zygopleura zygopleura* and *C. zygopleura varia* occuring in the Lower Campanian *pilula* and *Gonioteuthis quadrata* zones (zone/subdivisions 7 and 9).
Form 1a is restricted to the Upper Campanian with the 1b "normalform" present in the Weybourne Chalk (12) and a more strongly reticulate variant present in the Campanian Weybourne, Beeston and Paramoudra chalks (zone/subdivisions 12, 13, 14). Form 1b is present in the topmost Upper Campanian (Beeston and Paramoudra chalks). This gives way in the Lower Maastrichtian to form 2.

In the outcrop samples, the species exhibits a similar range to Herrig's material, but the ranges of some forms are slightly extended. Transitional forms were observed in the Lower Campanian *pilula* and *quadrata* zones (7 and 9) and into the lowest Upper Campanian basal *mucronata* Chalk (10). *C. zygopleura varia* form 1a is relatively common in the lower part of the Upper Campanian (Eaton and Weybourne chalks; zone/subdivisions 11, 12). Form 1b "normalform" is the most common form, extending from the basal Eaton Chalk to the Paramoudra Chalk (11-14). This form is especially common in the Beeston Chalk and the Paramoudra Chalk, with a less ornate variant (typified by Herrig's pl. 1, fig. 4) restricted to the Beeston Chalk at Caistor St Edmund, Norfolk. Smooth to poorly reticulate specimens of form 2 (Herrig, 1967, pl. 1, fig. 2) were recorded by Herrig as restricted to the Lower Maastrichtian; in Norfolk, they also occur in the Upper Campanian Paramoudra Chalk but are significantly more abundant in the Lower Maastrichtian at Sidestrand and Trimingham. The reticulate variant of form 2 is restricted to the Lower Maastrichtian.

The species was also present in its transitional form in two samples from the highest *coranguinum* Zone (Santonian) of Essex (SAG 2057, Witham Borehole; SAG 2058, Kelvedon Borehole).

Cythereis zygopleura zygopleura Pokorny, 1963.

Pl. 19, figs 14, 16.

1963 *Cythereis zygopleura* Pokorny, pp. 76-77, pl. 1, figs 1a-b, pl. 2.

1967 *Cythereis zygopleura zygopleura* Pokorny. Herrig, pl. 1, figs 7-9.

1968 *Cythereis (Herrigella) zygopleura* King, MS, pl. 15, figs 7-8..

1983. *Cythereis zygopleura zygopleura* Pokorny. Sivhed, pl. 2, fig. 13.

Diagnosis. Pokorny, 1963, gives an extremely detailed diagnosis. It will not be repeated here.

Dimensions.	L	H
LV (MPK 11686)	0.77	0.45
LV (MPK 11687)	0.75	0.40

Depository. MPK 11686, 11687.

Material. 10 specimens

Remarks. The present material is identical to specimens illustrated by Pokorny, Herrig and King. It is clearly distinguished from *C. zygopleura varia* by its smaller size and different ornament. The latter subspecies has a dentate, broadly rounded anterior margin with a clear marginal rib; the posterior margin is narrow and elongate and the sub-central tubercle is large, prominent and spherical with at least two spines. It is separate from the distinct median rib. The antero-lateral area is finely punctate in front of the sub-central tubercle and reticulate behind it. *C. zygopleura zygopleura* shows no antero-lateral puncta. The reticulation in this subspecies covers the entire lateral surface of the valve (see Herrig, 1967, pl. 1, fig. 9). In transitional forms (pl. 1, fig. 7) some puncta are present anterior of the subcentral tubercle.

Cythereis zygopleura expressa, recorded by Herrig (1967, pl. 2, figs 1-2) from the Upper Campanian of Northeastern Germany, is a larger, more strongly reticulate species than either *C. zygopleura zygopleura* or *C. zygopleura varia.* It was not seen in the present study.

Published range. Pokorny first recorded it from the Turonian of Bohemia, while Herrig reported it from the Coniacian of Northeastern Germany. The latter author notes that the species passes through a transitional stage in the Lower Campanian (also noted by King, 1968, MS, p. 175) into *C. zygopleura varia* in the Upper Campanian. Sivhed (1983) found it in the Lower Santonian to Lower Campanian at Malen Limestone Quarry, Southern Sweden.

Range in this study. In the Trunch Borehole, this species is not present in its typical Coniacian form (since this interval was not studied at this locality). It was also absent in the Santonian. In the outcrop samples, *C. zygopleura zygopleura* occurred in the Coniacian *coranguinum* Zone (zone/subdivision 3) at South Pickenham and Litcham (Norfolk) and across the basal *coranguinum* Zone (Norfolk) to low *coranguinum* Zone (Suffolk). It was also present in a single sample (SAG 14) from the lowest Santonian at Stowlangtoft, Suffolk, but in the majority of Santonian samples,

Cythereis sp. 1

Pl. 20, figs 18, 21.

Diagnosis. A sub-quadrate species characterized by its large sub-central tubercle and primary reticulate ornament with secondary punctation.

Dimensions.	L	H
LV (MPK 11710)	0.75	0.44

Depository. MPK 11710

Material. More than 20 specimens

Remarks. This species is left in open nomenclature due to its similarity to several Cretaceous species; it could not, however be assigned or compared to any one with any certainty.

Range in this study. The species was present in one sample of the highest *coranguinum* Zone (Santonian) from the Kelvedon Borehole, Essex. In the outcrop samples, it appears in the basal sample of the Coniacian *coranguinum* Zone (3) but is absent in the Santonian. It reappears in the Lower Campanian (Zone/subdivisions 7 and 9) and is also present in the Upper Campanian basal *mucronata* Chalk and the Eaton, Weybourne and Paramoudra chalks (10, 11, 12, 14). It also occurs in the Lower Maastrichtian pre- *Porosphaera* and *Porosphaera* Beds at Sidestrand. In the Trunch Borehole, the species is more sporadic in its range, occurring in the Lower Campanian *Gonioteuthis quadrata* Zone (9) and the Lower Maastrichtian.

Cythereis sp. 2

Pl. 21, fig. 19.

Diagnosis. A sub-quadrate species with a dentate anterior margin and a weakly developed reticulate network across its entire lateral surface; sub-central tubercle distinct.

Dimensions.	L	H
LV (MPK 11711)	0.72	0.38

Depository. MPK 11711

Material. 15 specimens.

Range in this study. In the outcrop samples, this species is present in the Upper Campanian basal *mucronata*, Eaton and Weybourne chalks and in the Lower Maastrichtian pre-*Porosphaera* Beds at Sidestrand. In the Trunch Borehole, it appears in the Lower Campanian *Gonioteuthis quadrata* Zone (9), in the Upper Campanian Weybourne Chalk and Lower Maastrichtian pre-*Porosphaera* Beds.

Cythereis sp. 3

Pl. 20, fig. 20.

Diagnosis. A sub-quadrate, rather heavily calcified species with a smooth lateral surface.

Dimensions.	L	H
LV (MPK 11712)	0.70	0.35

Depository. MPK 11712

Material. 9 specimens.

Range in this study. This species is present in the Upper Campanian at Cringleford (SAG 110), the Paramoudra Chalk at Whitlingham and the *O. lunata* Chalk at Trimingham (SAG 2001).
In the Trunch Borehole, it occurs in the Lower Campanian *G. quadrata* Zone (SAG 474).

Genus REHACYTHEREIS Gründel, 1973.

Generic Diagnosis. (Weaver, 1982, p. 79) "Valves strongly calcified, often large with a strong hinge ear; dorsal and ventral ribs not subdivided; dorsal rib usually ends in a large, block-like process, short median rib often separated from muscle node, which is not spinose. Lateral surface usually reticulate or pitted.

Table 2. 6. Diagnostic characteristics of the genus *Rehacythereis.*

Diagnostic feature	Remarks
Size, shape, ornament:	less inflated in dorsal view than *Cythereis*; valves often strongly calcified, often large with strong hinge ear, ornament reticulate or punctate, sometimes smooth.
Anterior marginal rib:	weakly developed
Dorsal rib:	dorsal and ventral ribs not subdivided, dorsal rib usually ends in a large block-like process or is weak and reduced
Eye tubercle:	size of eye tubercle varies from large and hemispherical to small and indistinct.
Sub-central tubercle:	non-spinose, often large and distinct.
Median rib:	short and often separated from sub-central tubercle.
Ventral rib:	dorsal and ventral ribs not subdivided, ventral rib usually weakly developed.
Hinge structure:	hemi-holoamphidont; anterior tooth high, smooth or crenulate; deep rounded anteromedian element, crenulate posterior tooth
Marginal zone, muscle scars:	marginal zone of moderate width; avestibulate, muscle scars consist of a vertical row of 4 elongate scars with a v-shaped antennal scar.

Rehacythereis sp. cf. *R. barringtonensis* Weaver, 1982

Pl. 20, figs 22, 23; pl. 21, fig. 1.

cf 1982 *Rehacythereis barringtonensis* Weaver, p. 80-81, pl. 11, figs 5-7.

Diagnosis. A small, elongate species with a small but distinct eye tubercle; posterior narrow and drawn out, weakly concave and slightly spinose on postero-dorsal slope; dorsal rib reduced to 5 spines ending in a small, block-like process; small tubercle situated halfway between postero-dorsal and postero-ventral spines. Median rib reduced to a single node behind large subcentral tubercle. Ornament consists of a series of regular shallow pits across the entire lateral surface.

Dimensions.	L	H
RV (MPK 11713)	0.52	0.29
RV (MPK 11714)	0.54	0.29
RV juv. (MPK 11715)	0.50	0.27

Depository. BGS catalogue numbers MPK 11713, 11714, 11715.

Material. 3 specimens.

Remarks. The material of the present study differs from Weaver's original species in its smaller size but is very similar in general shape and in the position of the sub-central tubercle and postero-ventral and posterodorsal spines. The ornament, which in the original species, occurs only on the posterior half of the lateral surface, covers the entire valve in the present material. The posterior shows the same slightly concave upper margin and straight, spinose lower margin but the lower margin in the present material consists of 4 spines which are longer than the four postero-ventral spines in the specimens illustrated by Weaver. The posterior is also more acute in the nominative species; in *R.* cf. *barringtonensis*, the posterior is broader and slopes downwards, making the ventral margin from the posteroventral spine to the terminal posterior spine appear concave.

R. paranuda Weaver, 1982 (pl. 12, figs 3-6), is larger and less elongate with a different ornament. Damotte, 1962, described and illustrates *R. divisa*, a species now reassigned to *Hazelina*. This is similar to *R. barringtonensis* in size and shape, but differs in certain other morphological details with "a large eye tubercle, a lower lateral ridge on the anterior rib which joins the anterior rib." (Weaver, p. 81)

Published range. (Weaver, 1982, p. 80) records his species from the Middle Cenomanian of Barrington, Cambridgeshire (type locality) and at various localities in Sussex, Hertfordshire and Kent.

Range in this study. This species is very rare and is restricted to the *coranguinum* Zone of the Coniacian and the Upper Campanian Paramoudra Chalk (outcrop zone/subdivisions 3 and 14).

Rehacythereis sp. cf. *R. cantabrigensis* Weaver, 1982

Pl. 21, figs 2-6.

cf 1982 *Rehacythereis cantabrigensis* Weaver, p. 81, pl. 11, figs 8-11.

Diagnosis. A medium species of *Rehacythereis* with a large, smooth, boss-like subcentral tubercle; reduced dorsal and ventral ribs, median rib reduced to a single small node between the ventro-dorsal and ventro-lateral spines; ornament covers entire lateral surface in the form of a series of regular and numerous small round puncta.

Dimensions.	L	H
Female LV (MPK 11717)	0.63	0.36
Male LV (MPK 11716)	0.67	0.33
Female LV (MPK 11718)	0.63	0.36
Female RV (MPK 11719)	0.64	0.36
Female LV (MPK 11720)	0.64	0.35
Juv. LV (SAG 183)	0.60	0.30

Depository. BGS catalogue numbers MPK 11716, 11717, 11718, 11719, 11720.

Material. 7 specimens.

Remarks. The material of the present study is very close to Weaver's description and figured specimens, but there are several differences in ornament, size and stratigraphical occurrence. It is larger and slightly less heavily calcified but very similar in shape and character of the ribs. The hinge ear in LV specimens

of *C. cantabrigensis,* as illustrated by Weaver (pl. 8, fig. 11), is more prominent and the anterior rib is more distinct and spinose. The eye tubercle is of a similar size but lacks the two short spines (1 in front, 1 behind) present in the material of this study. The ventral margin is straight and shows a clear marginal rib and postero-ventral spine; in *Rehacythereis cf. cantabrigensis*, this rib is reduced to a single spine preceding the backward facing postero-ventral spine. One of the diagnostic features of Weaver's species, seen clearly in both left and right valves, are the short, straight lines extending from the anterior marginal rib onto the lateral surface (6-7 in *R. cantabrigensis*). There are 6 similar lines of equal length and spacing in the material of the present study. The postero-dorsal and postero-ventral spines are longer than in Weaver's material. The sub-central tubercle is of a similar size and situation and is smooth and non-spinose in both cases. The ornament consists of regular punctation covering almost the entire lateral surface, but is shallower and much finer in the material of the present study.

Weaver (p. 75) describes *Planileberis foveata* (pl. 13, figs 17-20) from the Middle Cenomanian of Hertfordshire. This species is very similar to *R. cf. R. cantabrigensis* but is smaller and the lateral surface is more densely punctate. The broadly rounded anterior margin has a distinct, spinose marginal rib. The surface just behind this rib is entirely punctate and there is little sign of the short, straight ribs that are so evident in *R. cantabrigensis* and *R. cf. cantabrigensis.* The hinge ear is less well developed and, like the latter, bears two short spines immediately in front of and behind the small eye tubercle. The dorsal margin in *P. foveata* is straight and slightly spinose, but the posterodorsal spine is less than half the length of the postero-dorsal spine in the present material. The sub-central tubercle is much smaller and in the RV is indistinct. In the present material, this feature is large and prominent.

Published range. Weaver recorded his species from the Middle and Lower Cenomanian at several localities in Cambridgeshire, Kent and the Isle of Wight.

Range in this study. The species is uncommon and occurs in the Coniacian *coranguinum* Zone, Lower Campanian *O. pilula* and *Gonioteuthis quadrata* zones and in the Upper Campanian Weybourne Chalk. It was not found in the Trunch Borehole.

Rehacythereis sp. cf. *R. detrita* (Donze, in Donze & Porthault, 1972).

Pl. 21, fig. 7

cf 1972 *Cythereis detrita* Donze, p. 360-361, pl. 1, figs 1 – 5.

cf 1985 *Rehacythereis detrita* Donze & Porthault.. Babinot *et al.*, pl. 62, fig. 7.

Diagnosis. A large species of *Rehacythereis* with a small but prominent eye tubercle; anterior margin broadly rounded with anterior rib reduced to 7 short spines. Dorsal rib reduced to a row of very small spines with two larger postero-dorsal spines. Ornament non-reticulate; surface appears rough and slightly abraded.

Dimensions.	L	H
RV (MPK 11721)	0.75	0.40

Depository. MPK 11721

Material. One specimen; a second specimen lost during picking.

Remarks. The single specimen referred to this species differs slightly from that originally described by Donze and Porthault in its less elongate carapace and absence of an anterior marginal rib. Points of similarity include the broad anterior margin, indistinct median rib and sub-central tubercle, as well as the smooth, non-reticulate ornament. The specimen is possibly abraded, hence the rougher lateral surface.
Published range. Originally recorded by Donze & Porthault from the Lower Cenomanian of France. Babinot *et al.*, 1985 (p. 238) illustrate a single RV specimen from the French Lower Cenomanian.
Range in this study. Present two samples from the Santonian (SAG 19, 184), the single specimen available for study appears abraded and may, possibly, have been reworked. Its extreme rarity, however, means that there are no other specimens available for comparison.

Rehacythereis sp. 1.

Pl. 21, fig. 9.

Diagnosis. A medium, sub-quadrate species with a broadly rounded, spinose anterior margin with thick marginal rim; dorsal and ventral margins straight and non-spinose, sloping down to a narrow, depressed posterior with three short spines. Ornament smooth, lateral surface thickly calcified with a trace of a reticulate ornament in the anterior part of the valve.

Dimensions.	L	H
RV (MPK 11723)	0.65	0.36

Depository. MPK 11723
Material. Fewer than 5 specimens.
Remarks. Left in open nomenclature due to its rarity, this species cannot be compared to any other representative of the genus in this study.
Range in present study. Restricted to the Coniacian *coranguinum* Zone (3) of the outcrop samples.

Genus HERRIGOCYTHERE Gründel, 1973.

Generic diagnosis. See Gründel, 1973 (pp 1466-1467).
Remarks. Originally tentatively erected as a subgenus of *Idiocythere* Triebel, and based on the type species *Idiocythere definita* Herrig, 1965.
Range in this study. This is extremely rare, represented by a single specimen left in open nomenclature. It is restricted to one zone of the present study; the Lower Maastrichtian Grey Beds of Trimingham. In the literature, the genus is recorded as inhabiting warm, shallow marine environments.

?Herrigocythere sp.

Pl. 21, fig. 8.

Diagnosis. A medium, quadrate species; strongly calcified with a distinct hinge ear. Anterior margin broadly rounded with narrow marginal rim, two short spines on dorsal margin, first one behind small, spherical eye tubercle, postero-dorsal spine slightly longer. Posterior margin short and square; ventral margin with short, backward-facing ala. Lateral surface finely punctate.

Dimensions.	L	H
LV (MPK 11722)	0.54	0.29

Depository. MPK 11722

Material. 1 specimen.

Range in present study. Restricted to the Lower Maastrichtian Grey Beds of Trimingham.

Genus LIMBURGINA Deroo, 1966.

See table 2.7 (p. 242) for diagnostic features of this genus, compared and contrasted with *Oertliella* and *Curfsina*.

Limburgina sp. cf. *L. damottae* Babinot, 1980

Pl. 21, fig. 10.

cf. 1980 *Limburgina damottae* Babinot, pl. 37, figs 3-9

Diagnosis. A medium, quadrate species of *Limburgina*, with a close celate pattern of reticulation; broadly rounded anterior margin with narrow marginal rib; narrow spinose posterior; large sub-central tubercle especially in LV, in RV more obscured by ornament; ventral rib strongly developed and blade-like.

Dimensions.	L	H
Female LV (MPK 11724)	0.75	0.45

Depository. MPK 11724

Material. 5 specimens

Remarks. Babinot illustrates *L. damottae* from the Upper Santonian of Provence. This species has a similar form, size and ornament to *Limburgina binkhorsti*, also seen in this study, but the subcentral tubercle is more distinct and the valve more inflated. The present material is identical in shape and ornament to Babinot's original species, but is significantly smaller.

Range in present study. Restricted to the Upper Campanian Paramoudra Chalk of Whitlingham and Lower Maastrichtian pre-*Porosphaera* Beds at Sidestrand (Zone/subdivision 14, 15).

Limburgina binkhorsti (Van Veen, 1936)

Pl. 21, figs 11-17, 19

1936 *Cythereis binkhorsti* Van Veen, p. 133, pl. 1, figs 23-28.

1958 *Cythereis binkhorsti* (Van Veen). Howe & Laurencich, p. 185.

1968 *Oertliella binkhorsti* (Van Veen). Gründel, pl. 2, figs 16-18.

Diagnosis. A moderate to large species of *Limburgina*; ventral margin obscured by strongly developed crest-like rib with clear marginal carinae, spinose at its terminal point. Ornament regular reticulate; a series of open, polygonal alveoles. Sub-central tubercle small but distinct; slight longitudinal swelling posterior to tubercle. Posterior margin with a number of short marginal denticles.

Dimensions.	L	H

LV (MPK 11725)	0.75	0.36
RV (MPK 11729)	0.73	0.34
RV (MPK 11730)	0.73	0.34

Depository. MPK 11725 to 11731

Material. 30 specimens

Remarks. The present material closely resembles that illustrated by Howe & Laurencich which is a topotype specimen of Veen, 1936. The present material is, however, slightly larger and, in some specimens, a small longitudinal bar is present which is possibly a reduced median rib. This is not seen in earlier illustrations, which is why the species in this study is only compared to *L. binkhorsti.*

A similar species, *Limburgina ornata* of Bosquet, shows longitudinal swelling behind the subcentral tubercle but *L. cf. L. binkhorsti* can be distinguished by its smaller size and the presence of a stronger spine at the back end of the ventral rib (see Veen, p. 133). A form illustrated by Babinot, 1980, (pl. 37, fig. 10; pl. 38, fig. 1), *Limburgina* aff. *ornata,* from the French Upper Turonian, has a spinose termination on its ventral rib but is a larger species which bears three distinct spines on its posterior margin. Babinot also illustrates *L. damottae* from the Upper Santonian of Provence (pl. 37, figs 3-9). This species has a similar form, size and ornament to the present species but the subcentral tubercle is more distinct and the valve more inflated.

Published range. Van Veen first described the species from the Maastrichtian Tuffkreide of South Limburg; Gründel reports it from the Santonian of Austria.

Range in present study. The species is relatively common in the Upper Campanian to Lower Maastrichtian assemblages of this study and first appears in the Lower Campanian restricted *quadrata* Zone. It occurs in the Upper Campanian basal *mucronata* and Beeston Chalk (10, 13) and in the Lower Maastrichtian pre-*Porosphaera, Porosphaera* and Grey Beds (15, 16, 18).

Limburgina sp. cf. *L. senonensis* (Damotte, 1964)

Pl. 21, fig. 18

cf 1964 *Cythereis senonensis* Damotte, pl. 1, figs 3a-d; pl. 2, fig. 10.

cf 1968 *Quadracythere senonensis (*Damotte). King, MS, p. 250, pl. 27, figs 6, 7, 9.

1968 *Quadracythere* cf. *senonensis (*Damotte). King, MS, p. 253, pl. 27, figs 8-10.

cf 1971a *Cythereis senonensis* Damotte. Damotte, p. 75, pl. 4, fig. 4.

cf 1973a *Limburgina senonensis* Damotte. Colin, p. 151, pl. 14, fig. 1a-b.

cf 1980 *Limburgina* aff *senonensis* (Damotte). Babinot, p. 196, pl. 39, figs 2-4.

Diagnosis. A medium, quadrate species of *Limburgina,* ornament strongly reticulate consisting of regular, geometric polygons, rather heavily calcified. Anterior margin broadly rounded with narrow marginal rib with number of radial cross-ribs; dorsal margin straight, slightly converging posteriorly with concave ventral margin. Sub-central tubercle round and well-developed; median rib reduced or absent; ventro-lateral rib sub-parallel to ventral margin.

Dimensions.	L	H
LV (MPK 11732)	0.61	0.35

Depository. MPK 11732

Material. 5 specimens

Remarks. This species, referred to Damotte's species is almost identical in shape, size and ornament but differs in its stratigraphical range (uppermost Upper Campanian to Lower Maastrichtian. It is possible that this reflects an extended range for this species, which is why a full synonymy is given. King, 1968, MS, refers it to *Quadracythere* "with certain reservations". The illustrated specimens are, however, identical to the present material, which more closely conforms to *Limburgina*. King also illustrates *Quadracythere* cf. *senonensis*, distinguished by arbitary differences. It is included in the present study in synonymy with the nominative species. Babinot's *L.* aff. *senonensis* is also considered con-specific.

Published range. Santonian to Campanian; King, 1968 MS, gives a range of *coranguinum* Zone to Lower *mucronata* Zone, the species occuring in the Lower Campanian *Gonioteuthis* Zone in Norfolk.

Range in this study. This species is present in the uppermost Upper Campanian (Paramoudra Chalk) and the Lower Maastrichtian pre-*Porosphaera* Beds (zones 14, 15).

Limburgina sp.

Pl. 21, figs 19, 20, 21

Diagnosis. A medium, quadrate and strongly reticulate species; dorsal margin straight; anterior margin broadly rounded with clear marginal rib; ventro-lateral rib rather narrow and blade-like.

Dimensions.	L	H
LV (MPK 11733)	0.61	0.38

Depository. MPK 11733, 11734.

Material. 3 specimens

Remarks. Left in open nomenclature due to its extreme rarity and similarity to several other Cretaceous representatives of the genus. If more specimens had been available for study, the present material could be assigned to one of these previously published species.

Range in this study. Restricted to the Lower Maastrichtian pre-*Porosphaera* Beds of Sidestrand.

Genus SPINOLEBERIS Deroo, 1966.

Note. The genus *Spinoleberis* is characterised by its prominent subcentral tubercle, an ornament which may or may not be reticulate, ribs and alveoli in the posterior part of the valve and strong tubercle or spines at the posterior angles.

Range in this study. Extremely restricted in its stratigraphical range, occurring in the outcrop assemblages of the Coniacian low *coranguinum* and *coranguinum* zones.

Spinoleberis sp. cf. *S. ectypus* Babinot, 1973.

Pl. 24, fig. 5.

cf 1973 *Spinoleberis ectypus* Babinot, p. 42, pl. 5, figs 9-11.

Diagnosis. A medium species with a distinct, broad, curved ocular rib, a clear marginal rib and slightly tuberculate anterior margin; ventral margin partly obscured by spinose ventral rib with two short posteroventral processes. Median rib connects with prominent sub-central tubercle, curving up to the terminal postero-dorsal spine. Ornament reticulate; each fossa with a secondary ornament consisting of fine puncta. Posterior narrow, acute, with 4 short posteroventral spines. Posterior non-reticulate with fine puncta as primary ornament.

Dimensions.	L	H
LV (MPK 11779)	0.60	0.31

Depository. MPK 11779.

Material. 3 specimens.

Remarks. The material of this study differs from that of Babinot (1973, 1980) and Babinot *et al.*, (1985), in that the hinge ear is less pronounced and the dorsal margin is slightly less spinose. The angle between the terminal postero-dorsal spine and the posterior apex is less acute but, in all other aspects, the present specimens conform to Babinot's original material.

Spinoleberis sp. (Babinot, 1980, p. 152, pl. 26, figs 6-8) is similar in shape but is smaller and broader in the posterior; the ornament is also slightly different, the intercostal areas being smooth.

Published range. Babinot recorded his species from the Middle Turonian of France (1973 as in synonymy above) and from the Lower, Middle and lower part of the Upper Turonian (1980, p. 151, pl. 25, figs 16-17). It was later figured by Babinot *et al.*, 1985 (p. 238, pl. 62, figs 11-12). The later references are not included in the above synonymy because they are conspecific with Babinot's original species; the material of the present study is simply referred to it.

Range in this study. Restricted to the Coniacian low *coranguinum* Zone of Euston, Suffolk (SAG 16, 17); this species is extremely rare. It was not found in the Trunch Borehole or in any of the outcrop localities from Norfolk.

Spinoleberis tuberosa (Jones & Hinde, 1890)

(not illustrated)

1890 *Cythereis tuberosa* Jones & Hinde, p. 26, pl. 3, figs 2-3.

1978 *Spinoleberis tuberosa* (Jones & Hinde). Neale, pl. 17, fig. 8, p. 366.

Diagnosis. A medium species of *Spinoleberis*, with small rounded puncta in anterior part of valve and a distinct posteroventral spine. Primary ornament reticulate with large alveoli in posterior part of valve. Eye tubercle large, hemispherical; anterior margin and anterior rib spinose. Ventral margin straight, obscured by spinose ventral rib which is connected to median rib. Posterior spinose and acute with 5 short posterior spines.

Dimensions.	L	H
LV female? (SAG 113)	0.73	0.36

Material. 2 specimens (1 lost during curation)

Remarks. At 0. 73 mm in length, the measured specimen is smaller than the male left valve illustrated by Neale, 1978, from the Norfolk Chalk (L=0.82mm). This specimen may, therefore, represent a female specimen. Jones & Hinde quote a length of 0.70mm. In their monograph, Jones & Hinde also illustrate *Cythereis tuberosa symmetrica* (pl. 3, fig. 1) which from its size (0.52mm) and general ornament is clearly a juvenile.

Spinoleberis is quite common in the European Upper Cretaceous and many species can be found in the literature, all of which conform to Deroo's original diagnosis. A few of these species are worthy of mention. *Spinoleberis derooi* Damotte (1971, p. 6, fig. 4), from the Upper Campanian *Belemnitella mucronata* Zone of the Paris Basin, is of similar size and shape to *S. tuberosa* and exhibits the same positioning of the median rib, sub-central tubercle, dorsal spines, anterior rib and eye tubercle, but differs in its smooth intercostal surface. Damotte also records the presence of another species, *S. eximiodes* (Van Veen, 1936) from the same interval (1971, pl. 6, fig. 5, text figure 14a) but at 0. 60 to 0. 65mm in length, it is a significantly smaller species but is similar in general shape. However, it has fewer dorsal spines and the median rib is absent. Two postero-ventral spines replace the spinose ventral rib of *S. tuberosa* and the surface is smooth and non-reticulate. *Spinoleberis? aculeata aculeata* is figured by Donze & Thomel (1972, p. 380, pl. 3, figs 1-6) from the French Upper Cenomanian. It is also illustrated by Babinot *et al.*,1985 (p. 238, pl. 62, figs 9-10). This species is similar to the species in question, but is larger and the median rib is absent; the ornament is also finely reticulate and does not show the large alveoles and open reticulae seen in *S. tuberosa*. *Spinoleberis? aculeata obtusa* Donze & Thomel, 1972 (pl. 3, figs 7-10) from the French Cenomanian to Lower Turonian is a larger, less spinose species, with fewer dorsal spines; the median rib is absent and the ornament is more finely reticulate. A third species, left in open nomenclature by Donze & Thomel as *Spinoleberis?* sp. (pl. 2, figs 21-22) is also larger than *S. tuberosa* with a double row of anterior spines but only 2 postero-dorsal spines. The ornament is also less coarsely reticulate. *Spinoleberis ectypus* Babinot, 1973, illustrated by Babinot *et al.*, 1985, from the French Middle Turonian, also appears in the present study as a rare component in the Coniacian. This species is significantly smaller than *S. tuberosa* and differs in certain details of ornament; the anterior rib is less spinose in the former, there is s clear hinge ear with a larger and more hemispherical eye tubercle. The posterior is narrower and more acute. *Spinoleberis petrocorica* (Damotte, 1971) from the Cenomanian of the Paris Basin, as illustrated by Babinot *et al.*, 1985 (pl. 62, figs 13-17) differs both in size and shape to the species under consideration. The hinge ear in the LV is larger; the dorsal margin in this valve slopes down from the hinge ear, appearing almost concave and then straight. The posterior is more acute and narrower than in *S. tuberosa*. The right valve of Damotte's species resembles it more closely in shape. The anterior rib both valves is less spinose and the ornament is more coarsely reticulate. The median rib is less prominent in *S. petrocorica* and there is a secondary ornament of fine, regular punctae which are especially prominent in the anterior part of the valve. *S. tuberosa* also shows a secondary ornament but this is less distinct and covers the entire lateral surface of the valve.

Published range. The recorded range in Britain is Santonian, but most often Campanian or Lower Maastrichtian. Deroo, 1966, also recorded it from the Upper Maastrichtian of the Netherlands. Neale (1978) figures a specimen from the Norfolk Chalk; Jones & Hinde's original type locality for this species.
Range within this study.This species is extremely rare, coming from two samples from the Coniacian *Coranguinum* Zone of South Pickenham, Norfolk.

Genus MATRONELLA Damotte, 1974.

Generic diagnosis. Shape as in *Cythereis* but with longitudinal ribs reduced to row of spines or tubercles. Weaver (1982, p. 73) describes the pattern of muscle scars as "complex, with posterior branch of V-shaped antennal scar divided into two, as are upper two adductor scars typical of *Cythereis* to give 6 adductor scars." Surface between spines smooth.
Range in the present study. This genus occurs in the Coniacian and Upper Campanian in the outcrop assemblages. It appears in all three zones of the Coniacian, but is a Lazarus genus throughout the Santonian and Lower Campanian, reappearing in the Upper Campanian basal *mucronata,* Eaton, Weybourne and Beeston chalks.

Matronella matronae (Damotte & Grosdidier, 1963)

Pl. 22, figs 1-3.

non 1893 *Cythereis rudispinata* Chapman & Sherborne
1940 *Cythereis rudispinata* Chapman & Sherborne. Triebel, p. 200, pl. 4, figs 47-50.
1956 *Cythereis rudispinata* Chapman & Sherborne. Deroo, p. 1516.
1963 *Cythereis matronae* Damotte & Grosdidier, p. 57, pl. 3, fig. 7a-f.
1964 *Cythereis corrigenda* Kaye, p. 62, pl. 7, fig. 6, 9.
1966 *Cythereis corrigenda* Kaye. Gründel, p. 33, pl. 6, figs 7, 8.
1966 *Cythereis matronae* Damotte & Grosdidier. Gründel, p. 36, pl. 6, fig. 11.
1971a *Cythereis matronae* Damotte & Grosdidier. Damotte, p. 64, pl. 2, fig. 9.
1971 *Cythereis matronae* Damotte & Grosdidier. Keen & Siddiqui, p. 66, pl. 2, figs 5, 13.
1974 *Matronella matronae* (Damotte & Grosdidier). Damotte, pl. 23, figs 1-18; pl. 24, figs 19-22.
1976 *Matronella matronae* (Damotte & Grosdidier). Damotte, pl. 1, fig. 8; pl. 4, figs 37-39.
1978 *Matronella matronae* (Damotte & Grosdidier). Neale, pl. 17, figs 1-3, p. 366.
1982 *Matronella matronae* (Damotte & Grosdidier). Weaver, p. 73, pl. 13, figs 11, 12.
? 1982 *Matronella matronae* (Damotte & Grosdidier). Wilkinson & Morter, pl. 13.2, fig. 2.
1985 *Matronella matronae* (Damotte & Grosdidier). Babinot *et al.*, p. 235, pl. 60, figs 13, 14.

Diagnosis. A medium to large species of *Matronella* with strongly dentate anterior, ventral and postero-ventral margins. A rib bearing numerous tubercles closely parallels the anterior margin and becomes the ventro-lateral rib, bearing tubercles, of which the largest are sub-alar, and terminating on the caudal process. Two prominent tubercles occur posterodorsally; intercostal areas smooth; hinge hemiamphidont.

Dimensions.	L	H
LV (MPK 11738)	0.75	0.35
V (MPK 11738)	0.72	0.34
V (MPK 11739)	0.72	0.34

Depository. MPK 11737, 11738, 11739

Material. 4 specimens.

Remarks. Although the material of the present study are younger stratigraphically (Coniacian-Santonian compared to Albian to Cenomanian) and are slightly smaller, they are otherwise identical in shape and ornament to *M. matronae*, as illustrated by Damotte & Grosdidier and other authors. The specimens assigned to *C. rudispinata* by Triebel (1940) differ in size, shape and ornament from the species as first described by Chapman & Sherborne in 1893, which is larger and shows an indistinct surface reticulation. Kaye (1964) renamed these specimens, which are not conspecific with the earlier records, as *Cythereis corrigenda*. This species is included in synonymy with *M. matronella*, following such authors as Weaver, 1982, and others.

Colin (1973, p. 8), working on Upper Cretaceous assemblages from Southeastern France, describes a new subspecies, *Cythereis matronae exuberens,* (pl. 1, figs 13-14) from the Upper Cenomanian of the Dordogne. This subspecies is not, however, included in the synonymy of the present study, since it differs sufficiently from the original species. It is a more elongate species with long prominent spines; the carapace is more flattened, the median rib is absent and the dorsal rib is practically non-existent. *Cythereis (=Matronella) matronae matronae* Damotte & Grosdidier is less elongate than its subspecies, with a different ornament consisting of short, conical spines.

Cythereis buchlerae Oertli, 1958, from the Albian-Aptian of Provence is a larger and more heavily calcified species with a different ornament; the dorsal spines are also much shorter and less prominent. *Cythereis (Rehacythereis) sutterbyensis* Kaye & Barker, 1965, illustrated by Wilkinson (1988, MS., pl. 21, fig. 10) is similar in shape to *M. matronae,* with a double row of anterior spines but differs in its ornament; the dorsal rib is reduced to spines which are less prominent in *C. sutterbyensis*. The median rib is non-spinose.

Weaver, (1982, p. 65) describes the new sub-species, *Cythereis humilis humilis* from the Middle Cenomanian of Hertfordshire. Like *M. matronae,* the longitudinal ribs are reduced to a series of tubercles or spines but the former species is smaller and has a reticulate surface and a more complex pattern of muscle scars. Symmonds (MS., 1996, p. 213) describes *Matronella* sp. from the Lower Albian of Morocco. This species, which according to Symmonds, could have been accommodated within either *Spinoleberis* or *Matronella* based on its external morphology, differs from *M. matronae* in its more pointed posterior and more numerous and less regularly distributed spines. In dorsal view, *Matronella* sp. is very close to *M. matronae,* as illustrated by Keen & Siddiqui from the Cenomanian of Northern Ireland, but in lateral view, it is more sharply pointed posteriorly and has smaller spines, especially along the ventro-lateral rib. *M. matronae* is very like a species figured by Symmonds from the Lower Albian of Morocco. *Cythereis gemma* Symmonds, 1996 (MS., pl. 23, fig. 10, 11, 12) has a similar distribution of spines / tubercles and pore conuli, especially in the median rib but, in the case of the latter species, the ventro-

lateral and anterior marginal ribs are continuous, the tubercles are higher and more faceted, the dorsal and ventral margins are less parallel and the caudal area is longer and more symmetrical. *Rehacythereis lurmannae hannoverana* (Bertram & Kemper, 1971), from the German Albian, has a similar distribution of spines and tubercles in the median rib to the species currently under consideration, but the dorsal and ventral ribs are more slender and the anterior marginal rib lacks strongly developed tubercles.

Published range. Damotte & Grosdidier first described the species from the French Albian *Hoplites dentatus* Zone and the Middle to Lower Cenomanian. Wilkinson & Morter report the species from the Mundford C Borehole in the East Anglian Gault, while Neale, 1978, illustrates specimens from the Cenomanian of Northern Ireland.

Range in this study. Coniacian to Santonian.

Genus MAURITSINA Deroo, 1962.

Generic diagnosis. See Deroo, 1962.

Remarks. Liebau (1975) states that there are "nearly homeomorphic pairs of both *Cythereis* and *Mauritsina* and also examples of considerable intra-specific variations of the muscle field." In the present study, one species was originally assigned to *Mauritsina agedcumensis* of Damotte, 1964, based on the close similarity of size, age, shape and ornament. This species, however, differed only in the structure of its hinge and a new species was erected (*Cythereis campaniensis* sp. nov.), distinguished by its strong true- *Cythereis* type pentalobate, paramphidont hinge.

Range in this study. This genus exhibits a rather restricted stratigraphical range. In the outcrop assemblages, it occurs only in the Upper Campanian and is present in the basal *mucronata*, Eaton, Beeston and Paramoudra chalks.

Mauritsina lacertosa (Damotte, 1964)

Pl. 22, figs 6, 7, 9.

1964 *Cythereis lacertosa* Damotte, p. 102, pl. 1, fig 2a-d; pl. 2, figs 9a-b.

1968 *Cythereis (Herrigella) lacertosa?* Damotte. King, MS, pl. 13, figs 7, 8; pl. 15, figs 1, 2, 4.

1971a *Cythereis lacertosa* Damotte, pl. 4, fig. 3, text fig. 7c.

1985 *Mauritsina lacertosa* Damotte. Babinot *et al.*, p. 244, pl. 65, figs 2-3.

Diagnosis. A medium to large species of *Mauritsina* characterised by its V-shaped postero-dorsal loop and strongly vertical rib marking the posterior termination of the ventro-lateral rib; hinge holamphidont. See Damotte, 1964, p. 102, for more detailed diagnosis and description.

Dimensions.	L	H
RV (MPK 11742)	0.65	0.37
LV (MPK 11743)	0.66	0.38
LV (MPK 11744)	0.70	0.40

Depository. MPK 11742, 11743, 11744

Material. At least 30 specimens.

Remarks. King, 1968, MS, illustrates specimens that are very close to those of the present study, but are smaller and the lateral surface is smoother. The present material is very similar to that of Damotte.

Published range. Damotte, 1971, records the species from the Lower Campanian of the Paris Basin (*Actinocamax quadrata* Zone), continuing sporadically up into the basal Upper Campanian. Babinot *et al.*, 1985, also illustrate specimens from the Lower Campanian.

Range in this study. This species occurs in five of the eighteen zones (10, 11, 13, 14, 15) and ranges from the Upper Campanian basal *mucronata* Zone up to the Lower Maastrichtian pre-*Porosphaera* Beds. This may represent an extension of the published range. It occurs in the Eaton, Beeston and Paramoudra chalks (Upper Campanian), but was not seen in the Lower Campanian of either the Trunch Borehole or outcrop assemblages.

Genus MOSAELEBERIS Deroo, 1966.

Generic diagnosis. Moderate to large carapace; lateral surface smooth or reticulate; elongated longitudinal reticulations, longitudinal median rib. Hinge amphidont. Marginal zone with a number of straight or moderately sinuous marginal pore canals. Left valve overlaps right valve.

Taxonomic note. Pokorny (1978, p. 146) notes that the genus has a "characteristic adductor scar pattern in which the dorsal scar is divided, the dorso-median is the largest and the ventro-median and ventral are close to one another. Essentially the same pattern is seen in *Curfsina.*" In the material of the present study, the muscle scars were extremely difficult to see clearly and were of minor importance in generic identification. However, the adductor scar pattern is, in Pokorny's opinion, of phylogenetic interest attesting to "a similar norm of phylogenetic reactions, based on similar genetic constitution and is one more example of numerous parallel evolutionary trends that obscure the cladistic relations between the Protocytheridae, Trachyleberidae, Hemicytheridae and Cytherettidae." Many workers, however, do not agree with this (Whatley, *pers. comm.* September 1999). In the opinion of the present author, whatever trends do exist occur by coincidence rather than by design.

Phylogenetic relationships and, consequently, the systematic position of this genus was not definitely settled when Pokorny (1978) described 3 new species from the Upper Cretaceous of Czechoslovakia. Deroo (1966, p. 128) originally classified the genus within the Protocytherinae and assumed that the Protocytherinae corresponded to an incomplete lineage from *Protocythere* to *Veenia* and *Mosaeleberis*. Damotte (1971) places *Mosaeleberis* in the Trachyleberidinae, but Pokorny retains it provisionally within the Protocytherinae. The present study follows Damotte's classification within the Trachyleberidinae. The present author rejects Bertels designation (1975, p. 100) in which "*Mosaeleberis*, despite its clearly amphidont hinge, is here included in the Progonocytheridae, Progonocytherinae."

Generic range in this study. This genus ranges from Coniacian to Lower Maastrichtian in the outcrop assemblages. It appears in all three zones of the Coniacian and the Santonian *Uintacrinus* Zone, is a Lazarus genus in the Lower Campanian and is present in the Upper Campanian in the basal *mucronata*, Eaton and Beeston Chalk. In the Lower Maastrichtian it occurs in the *O. lunata* and Grey Beds of Trimingham and the Pre-*Porosphaera* Beds of Sidestrand.

Mosaeleberis dictyotos sp. nov.

Pl. 22, figs 10-12

1970 *Mosaeleberis* sp. Gründel, T1, figs 6-8

Derivatio nominis: Gr.

Holotype. LV, MPK 11748

Type Level. SAG 17, low *coranguinum* Zone, Coniacian.

Type locality. Euston, Suffolk.

Diagnosis. A medium species of *Mosaeleberis,* distinguished by its net-like reticulate ornament, inflated valves and double anterior rib; eye tubercle small but distinct; faint papillae in most solae.

Description. Medium; sub-quadrate in lateral view and inflated, greatest height at approximately mid-point. Eye tubercle small, spherical and prominent. Anterior margin in LV broadly rounded, apex at approximately mid-point, RV anterior margin less broadly rounded with apex below mid-point. Two narrow anterior marginal ribs present in both valves, parallel with smooth, non-denticulate anterior margin; dorsal and ventral margins straight, sloping down to the narrow posterior which is rounded in LV, slightly more acute in RV. Left valve larger than right valve. Three very small postero-ventral tubercles; small ventral rib partially obscures ventral margin. Primary ornament covers entire lateral surface, consisting of a fine, net-like regular reticulation; secondary ornament of fine papillae within each fossa. Sub-central tubercle absent in LV or obscured by ornament, very indistinct in RV. Sexual dimorphism not seen; all specimens adults.

Inner lamella quite narrow, wider at anterior; avestibulate; hinge line straight; muscle scars indistinct and partially obscured but conform to typical *Mosaeleberis* pattern as described by Pokorny (1978, p. 146); marginal pore canals not seen. Posterior tooth small and weakly crenulate, median element smooth; anterior tooth smooth.

Dimensions.	L	H
Holotype, LV (MPK 11748)	0.69	0.45
Paratype, LV (MPK 11745)	0.68	0.45
Paratype, RV (MPK 11746)	0.66	0.42
Paratype, RV (MPK 11747)	0.66	0.43

Depository. MPK 11745-11748

Material. 6 specimens (but see remarks).

Remarks. The 32 specimens of *Mosaeleberis* sp., Gründel, 1970, from the Middle Turonian of Saxony have been absorbed into *M. dictyotos* sp. nov., since they are believed to be conspecific. Although Pokorny included Gründel's material in synonymy with *Mosaeleberis interruptoidea,* the present author disagrees. Gründel's specimens are larger, with a finer ornament, with a double rib extending parallel to the broadly rounded anterior margin. This feature is also seen in the present species.

Pokorny (1978, p. 147) describes *M. interruptoidea* and *M.* ex. gr. *M. interruptoidea* (Van Veen, 1936) from the Lower and early Middle Turonian of Bohemia. The nominative species was originally

Pokorny (1978, p. 147) describes *M. interruptoidea* and *M.* ex. gr. *M. interruptoidea* (Van Veen, 1936) from the Lower and early Middle Turonian of Bohemia. The nominative species was originally recorded from the Maastrichtian of the Netherlands and is, in shape and general ornament, very similar to the present material, but differs in its smaller size (0.45-0.52mm in length). The ornament in the former species has larger reticulae and there is no double anterior marginal rib. Pokorny notes that, on examining several specimens from the Upper Maastrichtian, there are no important differences between these specimens and those in the Turonian of Bohemia. In view of the considerable age difference, future statistical investigations "may reveal differences of sub-specific rank." The present author believes it unlikely that the Turonian forms will prove conspecific with those from the Upper Maastrichtian and the Maastrichtian specimens of Van Veen (pl. 3, figs 31-36); Howe & Laurencich, 1958, (p. 206) and Deroo (1966, p. 131, pl. 18, figs 504 - 510) should be retained as *M. interruptoidea* and the Turonian forms revised as a new subspecies.

The type species, *Mosaeleberis interrupta* (Bosquet, 1847) differs from the present material in the pattern of reticulation and the presence of a clear median rib. Pokorny (1978, p. 153) discusses this species in detail and describes the ornament: "in the ventral intercostal field of *M. interrupta,* the longitudinal riblets are strong and dominating, being weakly developed only in the narrow stripe ventral to the median ridge." In the present species, the reticulate ornament covers the entire lateral surface and is equally developed throughout. The longitudinal riblets are well formed and distinct, but less strongly developed than in the type species or either of Pokorny's species from the Turonian of Bohemia. *M. crassa* (pp 153-154, pl. 5) has a large hinge ear in the left valve, with prominent median and dorsal ribs; it is also larger than the present species. *Mosaeleberis bohemica* (pp 149-153, pl. 2, figs 1-2; pl. 3, figs 1-4; pl. 4, figs 1-4, text figs 5, 6) is also a significantly larger species which differs in outline and the presence of a large hinge ear in the LV and a straight to slightly curved median rib extending from the sub-central tubercle. *M. propinqua* (Bosquet, 1854), as illustrated by Babinot *et al.,* 1985 (pl. 64, fig. 8) has a similar shape to the present species, with a double anterior marginal rib but intercostal areas are finely punctate and the eye tubercle is also smaller. The posterior margin is also more elongate, with 4 postero-ventral spines; the first two being twice the length as the others.

Bless, 1988 (p. 64, pl. 1, figs D, E; p. 66, pl. 2, fig. F) illustrates *M.* ex. gr. *rutoti* Deroo, 1966, from the Upper Campanian of South Limburg. This species is almost identical in shape and valve tumidity but has a smooth, featureless surface.

Range within this study. Restricted to the Coniacian outcrop samples. It is a rare species, present in only 4 samples in the basal *coranguinum* Zone at Newton-by-Castle-Acre, Norfolk, the low *coranguinum* Zone at Euston, Suffolk, and the upper part of the *coranguinum* Zone at South Pickenham, Norfolk.

Mosaeleberis macrophtalma (Bosquet, 1847)

Pl. 22, figs 13-19; pl. 23, fig. 1.

1847 *Cypridina macropthalma* Bosquet, p. 16, pl. 3, fig. 3a-d.

1854 *Cythere macropthalma* Bosquet, pl. 9, fig. 4a-d.

1860 *Cythereis macropthalma* Bosquet, p. 364

1936 *Cythereis macropthalma* Bosquet. Van Veen, p. 7, pl. 2, figs 43-48.

1938 *Cythereis macropthalma* Bosquet. Van Veen, p. 6.

1958 *Cythereis macropthalma* Bosquet. Howe & Laurencich, p. 212-213.

1964 *Cythereis macropthalma* Bosquet. Kaye, p. 64, pl. 6, figs 12-15, 17.

1965 *Mosaeleberis* cf. *macropthalma* (Bosquet). Damotte, pl. 6, figs 18-20.

1966 *Mosaeleberis macropthalma* (Bosquet). Deroo, p. 131, pl. 19, figs 514 - 516.

1971 *Mosaeleberis macropthalma* (Bosquet). Damotte, pl. 4, fig. 14, text fig. 10B.

1978 *Mosaeleberis macropthalma* (Bosquet). Neale, pl. 17, figs 13-15.

Diagnosis. A large, distinctive, rather quadrate species of *Mosaeleberis* with a large eye tubercle and prominent, separated low median rib and rounded sub-central tubercle; intercostal areas smooth; dorsal rib only present posteriorly; ventral rib narrow.

Dimensions.	L	H
LV female (MPK 11749)	0.69	0.39
RV female (MPK 11750)	0.71	0.39
LV male (MPK 11751)	0.73	0.37
Juv (A-1) SAG 2001	0.64	0.30

Depository. MPK 11749 - 11757

Material. More than 50 specimens

Remarks. Bosquet, 1847, first described the species from the Maastrichtian of Belgium. In 1967, Eager reviewed part of Bosquet's original collection of Cretaceous and Tertiary Ostracoda from France and Belgium. In this review, 1 syntype RV of *Cythere macropthalma* (NHM catalogue number I. 6534) is listed within the collections of the Natural History Museum, London (p. 20). The Cretaceous material was part of that used by Bosquet to describe the ostracod fauna from the Chalk of Maastricht.

The species shows sexual dimorphism and some morphological variation, the most important of which is size. The specimen illustrated by Van Veen and subsequently by Howe & Laurencich is significantly larger than those of other authors (L= 0.85mm). The material of the present study is slightly smaller than that figured by Neale, 1978 (a maximum length of 0.75mm, compared to 0.79mm), but the difference is well within the published range. Damotte, 1965, gives a range of lengths for adult specimens from the Campanian of the Paris Basin of 0.68 to 0.74mm. Late stage juveniles were also seen at 0. 65 mm in length. In the present study, similar sized juveniles were also recovered but a full ontogeny was not seen within the assemblages. Neale's specimens are identical to those of the present study and the species itself shows a wide morphological variability. Kaye, 1964, illustrates specimens from the Upper Campanian of Britain which differ slightly from those of Deroo, 1966. The general form is the same but the ventral, dorsal and median ribs are more pronounced. Damotte's 1965 and 1971a material conforms more closely to specimens figured by Kaye than that of Deroo and the material of the present study appears, on the whole, to be intermediate between the two.

Published range. The species is European in its distribution and is more common in Northern Europe; it is exclusively Upper Cretaceous, ranging through the Upper Chalk from the Santonian to Maastrichtian.

Santonian and Campanian: Neale (1978) records the species as present in the Chalk of Colchester, Essex and in the Upper Chalk of Norwich. In Britain, the range is Santonian and Campanian but this study will extend this from Santonian to Lower Maastrichtian.

Upper Campanian : Paris Basin *Belemnitella mucronata* Zone (Damotte, 1965, 1971; Babinot *et al.*, 1983); Northern Spain (Zarranga & Lazaro, 1990); England (Kaye, 1964).

Maastrichtian: Netherlands (Van Veen, 1936, 1938; Howe & Laurencich, 1958; Deroo, 1966); Belgium (Bosquet, 1847; Damotte, 1971).

Range in this study. In the Trunch Borehole, this species ranges from the Lower Campanian *Gonioteuthis quadrata* Zone (9) to the Lower Maastrichtian *Porosphaera* Beds. In the outcrop assemblages, the species exhibits a longer range. It first appears in the Coniacian *coranguinum* Zone (3) but is present in the Santonian only in the *Uintacrinus socialis* Zone. It is a Lazarus taxa in the *Marsupites* Zone and in the early parts of the Lower Campanian. It reappears in the *G. quadrata* Zone and is also present in the Upper Campanian basal *mucronata*, Eaton and Beeston chalks and the Lower Maastrichtian pre-*Porosphaera*, *Porosphaera*, *O. lunata* and Grey Beds of Sidestrand and Trimingham.

Mosaeleberis pseudomacrophtalma sp. nov.

Pl. 24, figs 2-7.

Derivatio nominis. The name of this species reflects its similarity to *M. macropthalma*.

Holotype. Female, left valve (MPK 11758)

Type level. SAG 115, Coniacian *coranguinum* Zone

Type locality. South Pickenham, Norfolk.

Diagnosis. A medium species of the genus, characterised by its broadly rounded anterior margin and a large hinge ear in the LV which is absent in the RV; dorsal margin straight, ventral margin partially obscured by ventral rib; four to five short ventro-posterior spines or denticles. Sub-central tubercle large and prominent, separate from short, thick median rib; intercostal areas smooth.

Description. Medium. Sub-quadrate in lateral view; carapace fusiform in dorsal view. Anterior margin broadly rounded with faint rib and several indistinct tubercles; apex at approximately mid-height; LV larger than RV with clear overlap. LV with large hinge ear, dorsal margin behind hinge ear straight. RV smaller; hinge ear absent, dorsal margin entirely straight. Eye tubercle hemispherical and distinct, less so in right valve. Ventral margin in both valves partially obscured by a narrow rib; four to five small postero-ventral denticles; posterior acute. Sexual dimorphism distinct, males more elongate and less inflated, females slightly higher and less elongate, posterior broader and less acute. Sub-central tubercle small but distinct, hemispherical; greatest height at mid-length; short, thick median rib separate from sub-central tubercle extending almost to the posterior; intercostal areas smooth. Early ontogeny unknown, some late-stage juveniles present.

Inner lamella relatively narrow anteriorly, broader at posterior; marginal pore canals not seen; hinge amphidont; anterior tooth in LV smooth and slightly peg-like, smooth median element, posterior

tooth simple and smooth; RV complementary. Muscle scars indistinct but show a typical trachyleberid arrangement

Dimensions.	L	H
Holotype, female, LV (MPK 11758)	0.65	0.43
Paratype, female, RV (MPK 11759)	0.63	0.42
Paratype, female C (MPK 11760)	0.65	
Paratype, female RV (MPK 11761)	0.62	0.42
Paratype, ?juv. RV (MPK 11762)	0.60	0.39
Paratype, male RV (MPK 11763)	0.68	0.44

Depository. MPK 11758-11763.

Material. 12 specimens.

Remarks. This species is similar to *M. macropthalma* (Bosquet, 1847) but has a much larger hinge ear in the LV and a stronger median rib; it is significantly smaller, with a more restricted stratigraphical range (Coniacian to uppermost Lower Campanian/basal Upper Campanian). The latter occurs in the Santonian to Campanian in British records (Neale, 1978, p. 366) and in the Upper Coniacian to Lower Maastrichtian in the Upper Chalk of Norfolk (this study). The present species ranges from 0. 63 to 0. 68 mm in length; adult specimens are the same size as juveniles of *M. macropthalma* (adults ranging from 0.73 to 0.76mm). If these specimens did not exhibit a typically adult hingement, they might be considered as the juvenile form of *M. macropthalma;* differences in size and ornament, however, make this unlikely. The present author is satisfied that the two are not conspecific.

Range in this study. The species ranges in the outcrop assemblages from the Coniacian to topmost Lower Campanian / basal Upper Campanian in Norfolk, although absent in the Santonian. It was present in the *coranguinum* Zone at South Pickenham, in the Lower Campanian restricted *quadrata* Zone at Stiffkey (locality 1, absent at locality 2), the *pilula* Zone at Wells and in the topmost restricted *quadrata* Zone (upper Lower Campanian) or the basal *mucronata* Zone at Bawburgh, Norfolk.

Genus OERTLIELLA Pokorny, 1964

Table 2.7 (p. 241) and table 2.8 list the diagnostic characteristics *Oertliella, Limburgina* and *Curfsina.*

Range within this study. First appears in the outcrops in the low *coranguinum* Zone of the Coniacian but is a Lazarus genus throughout the Santonian and much of the Lower Campanian, reappearing in the restricted *quadrata* Zone. It occurs in the Upper Campanian basal *mucronata,* Weybourne and Paramoudra chalks and in the Lower Maastrichtian Grey Beds of Trimingham. The genus *Limburgina* has a more restricted range and first appears in the outcrop assemblages, in the restricted *quadrata* Zone of the Lower Campanian and ranges up into the Lower Maastrichtian *Porosphaera* Beds of Sidestrand.

Oertliella sp. cf. *O. pulchra* Babinot, 1980.

Pl. 23, fig. 8.

Table 2.7. Genus *Oertliella* Pokorny, 1964:

Type species = *Oertliella reticulata* (Kafka)

	original type description, Pokorny, 1964	emend. Benson, 1972 - to include a greater range of species development than was considered by Pokorny	Weaver, 1982
eye tubercle	not considered or mentioned in original type description	present - an important addition to the diagnosis	not mentioned, but Weaver's illustrated specimens do show clear ocular tubercles
ornament, shape, size	not mentioned, strongly reticulate	not mentioned, strongly reticulate with surface sculpture of the last larval stage being already very similar to that of the adult	
anterior marginal rib	narrow	narrow, without ocular ridge	narrow
dorsal rib	originates through the strengthening of reticulation riblets, low or reduced to several spines	originating througth the strengthening of several muri of the reticulum - low, reduced to spines or with an elongate crest formed by the fusion of the spines or extension of the carinae	present or reduced to several spines
median rib	absent	absent	well developed
ventrolateral rib	strong, well developed already in later larval stages	weak or strong and may be wide and crest like in species where the marginal carinae are well developed	not mentioned but illustrated specimens show this feature to conform to original diagnosis and Benson's 1972 emend.
hinge	amphidont; faint crenulations of terminal teeth of RV, anterior tooth slender, median hinge element smooth	hinge amphidont , with faint crenulations of the terminal teeth of the RV; anterior tooth slender, with base distinctly shorter than height; median hinge element smooth	in RV weakly crenulate terminal teeth and smooth median groove
muscle scars and internal features	antennal scars in front of adductors - v-shaped	duplicature narrow to medium in width, numerous straight radial pore canals; antennal	not mentioned

Table 2.8. Diagnostic features of *Oertliella*, *Curfsina* and ***Limburgina*** compared and contrasted.

genus and author	*Oertliella* Pokorny, 1964	*Limburgina* Deroo, 1966	*Curfsina* Deroo, 1966
type species	*Oertliella reticulata* (Kafka)	*Limburgina ornata* (Bosquet)	*Curfsina major* (van Veen, 1936)
eye tubercle	present	present, distinct	present, hemispherical on frontal lobe with ocular ridge
size, shape, ornament	medium in size, sub-rectangular in outline; reticulate	small to large in size; ornament reticulate, intercostal surface covered with polygonal alveoles	medium to small size; ornament reticulate, intercostal areas smooth or irregularly ornate,, ridged, reticulate, spinose or punctate
anterior marginal rib	narrow, without ocular rib	variable	present, sometimes bearing elongate pits - as in *C. derooi* of Weaver, 1982; clear frontal lobe and ocular ridge
dorsal rib	originating through the strengthening of several muri of the reticulum; low, reduced to spines or extension of the carinae	dorsal margin usually hidden by dorsal rib	present, rarely divided into spines, often with vertical processes at their posterior ends
sub-central tubercle	present, rounded and may be prominent or indistinct	hemispherical - may or may not join onto median rib	rounded or slightly elongate - may or may not join onto the median rib
median rib	usually absent	present, may or may not join sub-central tubercle	present, may or may not join subcentral tubercle
ventrolateral rib	strong to weakly developed ; may be wide and crest-like in species where the marginal carinae are well developed	distinct, usually well developed and may be crest-like, as in *Oertliella*, where the marginal carinae are well developed	may join anterior rib, rarely divided into spines - often with vertical processes at their posterior ends
hinge structure	hemi-hol' amphidont; weakly crenulate teeth and smooth median element in RV, anterior tooth elongate and slender	in RV long, high smooth anterior tooth; median element smooth; posterior tooth usually crenulate	in RV long anterior tooth, smooth median element, elongate, crenulate posterior tooth
other internal features, muscle scars	duplicature narrow-wide, RPC numerous antennal scars in front of undivided adductors, v-shaped frontal	in RV long, high anterior tooth is smooth, median element smooth, posterior tooth usually crenulate	inner lamella and marginal zone moderately wido with a number of MPC; 4 adductors, v-shaped antennal scar

cf 1980 *Oertliella pulchra* Babinot, pp 186-188, pl. 34, figs 1-8; pl. 35, figs 1-13.

Diagnosis. A medium, sub-quadrate and moderately heavily calcified, ornate species of *Oertliella*, with an open reticulate network.

Dimensions.	L	H
MPK 11764	0.75	0.47

Depository. MPK 11764.

Material. 3 specimens.

Remarks. The present material is very similar to Babinot's species, recorded from the Santonian of Provence, but is significantly smaller and is restricted to the Upper Campanian and Lower Maastrichtian, It may represent a closely related species or sub-species.

Range in this study. This species is restricted to the Upper Campanian outcrop samples, where it occurs in the basal *mucronata* Zone Chalk and the Paramoudra Chalk (zone/subdivision 10, 14) and Lower Maastrichtian Grey Beds of Trimingham (18). It does not occur in the Trunch Borehole.

Genus PLANILEBERIS Deroo, 1966.

Generic diagnosis. Weaver, p. 75, "Size variable, shape subrectangular but strongly laterally compressed. Muscle node weak, middle rib absent. Surface reticulate or pitted."

Range within this study. Appears in the outcrop assemblages in the Coniacian low *corangulnum* Zone but is a Lazarus genus throughout the Santonian and much of the Lower Campanian, reappearing in the restricted *quadrata* Zone. In the Upper Campanian, it occurs in the Beeston and Paramoudra chalks and also in the Lower Maastrichtian Grey Beds of Trimingham and the pre-*Porosphaera* Beds of Sidestrand.

Planileberis parva

Pl. 23, figs 9, 10.

Diagnosis. A small, reticulate species of *Planileberis*, with a rounded anterior margin and broad marginal rib, sloping to narrow, pointed posterior, ventral rib reduced, median and dorsal ribs absent.

Dimensions.	L	H
(MPK 11765)	0.43	0.19
(MPK 11766)	0.41	0.19

Material. 5 specimens.

Published range. Upper Chalk of the Netherlands and Denmark.

Range in this study. Restricted to the Lower Maastrichtian pre-*Porosphaera* Beds of Sidestrand.

Planileberis sp. cf. *P. rectangularis* Collin, 1973

Pl. 23, figs 11, 13.

Diagnosis. A subquadrate species of *Planileberis* with a smooth – weakly reticulate ornament, reduced median rib and prominent eye tubercle.

Dimensions.	L	H
MPK 11767	0.61	0.27

Material. At least 15 specimens.

Published range. Cenomanian of France.

Range in this study. In the Trunch Borehole, this species is restricted to the Lower Maastrichtian. In the outcrop samples, it ranges from the Upper Campanian Weybourne Chalk into the Lower Maastrichtian Grey Beds at Trimingham.

Planileberis subparva (Pokorny, 1967)

Pl. 23, figs 12, 15

1967c *Curfsina subparva* Pokorny, p. 345

Diagnosis. A subquadrate species of *Planileberis* with a large eye tubercle and a reticulate ornament.

Dimensions.	L	H
C (MPK 11769)	0.51	0.21
RV (MPK 11832)	0.49	0.20

Depository. MPK 11769, 11832

Material. More than 30 specimens.

Published range. Pokorny records the species from the Upper Chalk of Bohemia.

Range in this study. In the Trunch Borehole, this species ranges from the Lower Campanian *O. pilula* Zone (7) and *Gonioteuthis quadrata* Zone (9) up into the Lower Maastrichtian *Porosphaera* Beds (Zone/subdivision 16). In the outcrop assemblages, it exhibits a longer stratigraphical range; it first appears in the Coniacian *coranguinum* Zone (3) but is absent throughout the Santonian and reappears in the Lower Campanian and extends into the Lower Maastrichtian *Porosphaera* Beds.

Genus PLATYCYTHEREIS Treibel, 1940.

(junior synonym *Chapmanicythereis* Gründel, 1973)

Treatise reference. Q 339

Treatise diagnosis. "Hinge hemiamphidont. Sides flat, much compressed; subcentral tubercle bladelike, deflected backward. *L. Cret.-Upper Cret.*"

Clearly, the generic diagnosis, as it appears in the *Treatise*, is inadequate and needs extending to cover the main diagnostic points by which the genus may be distinguished from other laterally compressed forms. It is the ornament that is most characteristic but this also can be variable. The majority of forms, however, do show a spongeous reticulation and blade like ribs.

Weaver, 1982, p. 77: "Size moderate to large, subrectangular in outline, strongly laterally compressed. Hinge ear not developed. Surface of valves covered with "spongy" reticulation, ribs often formed as raised frills. Anterior margin often with strong spines."

It should be noted, however, that such spongy reticulation is only seen in adult specimens (See also Van Morkhoven, 1963, p. 192-195).

Remarks. The genus was originally assigned to Cytherinae until Sylvester-Bradley (1948) erected Trachyleberididae, Trachyleberinae. Triebel based the genus on the type species *Cythereis excavata* of Chapman & Sherborne, 1893, but there has been much confusion regarding this problematic species. Chapman (1898, p. 336, fig. 2, line drawing x 40) illustrates a LV specimen of *Cythere gaultina* Jones *excavata* Chapman & Sherborne, from the "Cambridge Greensand" (Upper Gault), which is linked in synonymy to *C. excavata*. The marginal ridge is slightly less distinct and continuous than in *P. cribrosa* and the reticulate ornament on the flattened lateral surface is more open. *P. excavata* varies from the species assigned to the genus in the present study but are similar in size, shape and lateral compression of the carapace. Kaye (1964) considers the specimens of Chapman & Sherborne to be conspecific with "*Cythereis" gaultina* Jones, 1849, which effectively becomes the type species, since it has seniority. Triebel, 1940, took Chapman's 1898 figures as typical of the type species but these are not conspecific with *C. gaultina*. Kaye (1964) renamed such species *Platycythereis chapmani*.

The present author agrees with Weaver in questioning the validity of Grūndel's 1973 genus *Chapmanicythereis,* distinguished from *Platycythereis* by the presence of an eye tubercle and longitudinal ribs. Weaver (p 78) states that " the development and strength of lateral ribs, however, is variable even within the genus *Chapmanicythereis* and I prefer to regard all species with a spongeous type of reticulation as belonging to *Platycythereis."*

Pokorny (1967) published a detailed research paper entitled " the genus *Platycythereis* Triebel, 1940 (Ostracoda, Crustacea) in the Upper Cretaceous of Bohemia." In this work, he describes *Platycythereis cribrosa* Triebel *bohemica* subsp. nov. from the Lower Turonian, which " differs from the nominative species in some minor sculptural features such as the continuation of the blade-like marginal ridge of free margin onto the posterior part of the dorsal margin, and shows a great variability of sculpture which, in some cases is primary, in others clearly due to the state of preservation." Pokorny notes that, in a worn carapace, the marginal ridges almost disappeared as well as the outgrowths of the lateral surface. At the time of Pokorny's 1967 paper, the genus *Platycythereis* "so far known to the author has been recorded from the Lower Cretaceous, up to the Lower Turonian. The occurrence in the lower part of the Middle Turonian is thus the youngest known." *P. cribrosa bohemica,* with its continuous blade is more primitive than the forms where this ridge is represented by isolated outgrowths and, indeed, Middle Turonian specimens often show a "more or less dissolved" marginal ridge. This evolutionary trend, if continued through to the Coniacian and the restricted *quadrata* Zone of the Lower Campanian, would explain the very poorly developed ridge and weak ornament of the species assigned to the genus in the present study. If Pokorny's figured specimens are examined in sequence, pl. 1, figs 1-2 shows an ornate, reticulate species with a clear, blade-like marginal ridge, especially clear in the female holotype. *Platycythereis cribrosa* subsp. indeterminable (pl. 2, fig. 3) has a slightly less developed ridge; both forms show a very clear ocular tubercle and strong lateral compression. The specimens assigned to the genus in this study show the flattened, compressed lateral surface and hemiamphidont hinge. They fall within the size range of previously published species. The eye tubercle is generally smaller and less distinct. The ornament is indistinct and only weakly reticulate. In most cases, the lateral surface appears rough with only a few remaining traces of a reduced marginal rib. It is possible that such specimens

represent worn individuals of an ornate species in the *P. cribrosa* group or reflect the phylogenetic trend towards reduced ornament suggested by Pokorny.

Pokorny notes that larval stages show a merodont hinge and often have "all the elements of the gross sculpture", but recorded measurements for juvenile instars were 0. 56 - 0.59mm in length. The size of the present material identifies them as adults. Gründel, 1969 (pl. 1, fig. 15) illustrates a specimen (adult or late stage juvenile) of *Platycythereis cribrosa* Triebel, 1940, from the Plenus Zone of Saxony. Although the quality of the plates in the 1969 publication seen by the present author were not good (a poor photocopy), the figured specimen shows a flattened carapace with a blade-like marginal ridge and reticulate ornament. It appears to be a left valve. In the opinion of the present author, Gründel's specimen of *P. cribrosa* is conspecific with Triebel's material, but is possibly a late stage juvenile.

Mertens, 1956, describes and illustrates three species from the Albian /Cenomanian of Northwestern Germany (*P. gaultina* (Jones, 1849), *P. degenerata* Triebel, 1940, and *P. triebeli* Mertens. *Platycythereis degenerata* from the Middle to Upper Albian (1940, Triebel, pl. 8, figs 93-98; 1956, Mertens, p. 210, pl. 12, figs 82-85; 1958, Howe & Laurencich, p. 459; 1966, Gründel, pl. 7, fig. 17, and others) has a reticulate surface but does not show distinct marginal ridges and, like the material of the present study, the eye tubercle is not prominent. *Platycythereis gaultina*, with a range of Lower to Upper Albian (figured by authors such as 1940, Triebel, pl. 7, figs 81-85, pl. 8, figs 86-87; 1956, Mertens, pl. 11, figs 59-60; 1958, Howe & Laurencich, p. 460; Gründel, 1966, pl. 7, fig. 18) and from the Albian / Cenomanian boundary (Wilkinson, 1988, pl. 2, fig. 9). *P. gaultina* is, from published records, smaller than the present material (L= 0.55 mm compared to an average of 0. 63 mm). The poor quality of Merten's figures (only one dorsal view of a complete carapace and a single RV are illustrated, in which the ornament is not distinguishable) makes it difficult to know if this material is conspecific with Jones' (1849) and Jones & Hinde's (1890) nominative species. The 3rd species, *P. triebeli* Mertens, (also illustrated in Howe & Laurencich, 1958, p. 461) is a short-lived species occurring across the Middle to Upper Albian boundary. In this species, the marginal ridge is not continuous, but is more distinct than in the present material; lateral ornament reticulate, marginal denticles more numerous; broader anterior margin and posterior is truncate and less obliquely pointed than the species left in open nomenclature in this study.

Generic range in this study. It can be said that the forms seen in the present study are not true-*Platycythereis* in that they do not show a spongeous ornament. They occur at a later stratigraphical date than the previously published Turonian limit for the genus. Weaver (1982, p. 100) notes that, in the Cenomanian of Southern England, marked changes occur at both specific and generic level. *Platycythereis* "can be found in post-Cenomanian deposits from other areas but in Southern England disappears at the same level in all the areas studied." The genus occurs rather sporadically in the present study, present in the Coniacian *coranguinum* Zone and the Lower Campanian restricted *quadrata* Zone. All are laterally compressed and show evidence of marginal ridges. They represent *Platycythereis sensu lato;* the end product of a gradual decline in ornament noted by Pokorny (1967), juvenile specimens (which are known to exhibit no spongy reticulation), badly abraded or reworked adults of a usually ornate earlier species, or belong to a very closely related genus. In the present study, however, the genus is a rare component and such individuals will be retained in *Platycythereis*.

Pl*atycythereis ? sp. 1*

Pl. 23, fig. 14

Diagnosis. A laterally compressed species with a broad anterior margin and very narrow posterior; a clear narrow anterior rib joins with a similar ventral rib. Ornament rather pustulose.

Dimensions.	L	H
(MPK 11770)	0.56	0.27

Depository. MPK 11770

Material. Fewer than 5 specimens

Remarks. Left in open nomenclature due to its rarity and uncertain generic position; this species is tentatively assigned to *Platycythereis* because of its lateral compression and reduced marginal ridge. It does not resemble any Cretaceous representative of the genus and its post-Turonian occurrence would exclude a *sensu stricto* designation. The specimens are possibly juvenile or reworked / abraded adults.

Range in this study. Restricted to the Coniacian *coranguinum* Zone.

Platycythereis ? sp. 2

Pl. 23, fig. 16

Diagnosis. A laterally flattened species with a dentate anterior margin and an oblique posterior. Ornament appears "overgrown" or residual.

Dimensions.	L	H
RV (MPK 11771)	0.45	0.20

Depository. MPK 11771

Material. 1 specimen.

Remarks. Left in open nomenclature due to its uncertain generic position; this species is tentatively assigned to *Platycythereis* because of its lateral compression and reduced marginal ridge. It does not resemble any Cretaceous representative of the genus and its post-Turonian occurrence would exclude a *sensu stricto* designation. The specimens are possibly juvenile or reworked / abraded adults.

Range in this study. Restricted to the Coniacian *coranguinum* Zone in the outcrop assemblages.

Platycythereis ? sp. 3

Pl. 23, fig. 17.

Diagnosis. A laterally compressed species with a broad dentate anterior margin and narrow posterior; 5 antero-ventral spines; two posterior spines; a clear narrow anterior rib connects with a reduced ventral rib. Ornament reticulate/spongy; clear sub-central tubercle.

Dimensions.	L	H
(MPK 11772)	0.62	0.25

Depository. MPK 11772

Material. 1 specimen

Remarks. Left in open nomenclature due to its rarity and uncertain generic position; this species is tentatively assigned to *Platycythereis* because of its lateral compression and reduced marginal ridge. It does not resemble any Cretaceous representative of the genus and its post-Turonian occurrence would exclude a *sensu stricto* designation. The specimen is possibly a reworked/abraded adult.

Range in this study. Unlike the other two species in the present study, restricted to the upper Coniacian; this species cccurs in the Lower Campanian *quadrata* Zone. It was not present in the Trunch Borehole.

Genus PTERYGOCYTHEREIS Blake, 1933.

Treatise reference. Q267.

Treatise diagnosis. "Carapace rather inflated ventrally, with strong, pointed alae; lateral surface generally smooth and, in most species, bearing a blade-like dorsal ridge; eye spot distinct; anterior and pposterior spiny; ventral surface flattened and usually bearing longitudinal ribs. Hinge typically holamphidont, but in some European species, median elements may be crenulate; adductor scars in vertical row of four. Antennal scar V-shaped, mandibular scar oval."

Weaver, 1982, gives the following diagnosis: "Outline sub-rectangular in lateral view, arrow shaped in dorsal view due to alar projections in the ventrolateral region. Hinge of right valve with high anterior tooth which may be smooth or stepped, postjacent rounded socket, crenulate or smooth median bar and fairly high, smooth to weakly crenulate posterior tooth."

Remarks. The taxonomical position of *Pterygocythereis*, *Pterygocythere* and *Alatacythere* has already been discussed and will not be repeated.

Range of genus in the present study. *Pterygocythereis* ranges in the outcrop assemblages from the Lower Campanian restricted *quadrata* Zone to the Pre-*Porosphaera* Beds of the Lower Maastrichtian *B. lanceolata* Zone. It is absent in the Upper Campanian Paramoudra Chalk and Lower Maastrichtian *O. lunata* Chalk (i.e. across the Campanian - Maastrichtian boundary), but reappears again in the basal *mucronata* Chalk, Eaton, Weybourne and Beeston chalks of the Upper Campanian *B. mucronata* Zone. This mirrors the stratigraphical range of the genus *Pterygocythere* almost exactly. *Alatacythere*, however, has a wider range: Coniacian low *coranguinum* Zone to Lower Maastrichtian Pre-*Porosphaera* Beds but this last genus exhibits Lazarus absences throughout the Santonian and much of the Lower Campanian.

Pterygocythereis phylloptera phylloptera (Bosquet, 1854)

Pl. 23, fig. 18; pl. 25, figs 1-4, 6, 7.

1854 *Cythere phylloptera* Bosquet, p. 116, pl. 7, fig. 10a-d.

1890 *Cytheropteron? phyllopterum* (Bosquet). Jones & Hinde, p. 37, pl. 3, figs 9-10.

1940 *Cythereis (Pterygocythereis) phylloptera* (Bosquet). Bonnema, p. 132, pl. 4, figs 37-41.

1958 *Pterygocythereis? phylloptera* (Bosquet). Howe & Laurencich, p. 486.

1964 *Alatacythere phylloptera* (Bosquet). Kaye, pl. 2, figs 17, 19.

1965 *Pterygocythereis phylloptera* (Bosquet). Herrig, text fig. 80, p. 833.

1978 *Pterygocythereis phylloptera* (Bosquet). Neale, pl. 16, figs 14-18.

1985 *Pterygocythereis phylloptera* (Bosquet). Robaszynski *et al.*, p. 112, pl. 22, fig. 1.

Diagnosis. A medium species of *Pterygocythereis*; prominent eye tubercle, anterior margin rounded with 11-12 short spines, three longer spines on the straight dorsal margin and four postero-ventral spines; alar process narrow with subsidiary spines along its crest; lateral surface smooth.

Dimensions.	L	H
LV (MPK 11773)	0.65	0.27
LV (MPK 11774)	0.62	0.24
LV A3 Juv. (MPK 11776)	0.55	0.21
LV (MPK 11777)	0.66	0.27

Depository. MPK 11773 to 11777

Material. More than 50 specimens.

Remarks. Bosquet's original specimens are, according to Jones & Hinde (1890) very similar to those from the Chalk of Northern Ireland but some specimens had "a smoother anterior front margin and a more spinose projection on each valve." The present material has more pronounced marginal spines although some specimens were identical to those figured by Jones & Hinde. They are very similar to those figured by Robaszynski *et al.*, 1985, but exhibit more pronounced denticles on the anterior and posterior margins. The alar process is more strongly developed. Juveniles appear very close to those figured by Bosquet and Howe & Laurencich (1958, p. 486).

Pterygocythereis phylloptera (Bosquet) *reducta* Weaver, 1982, (pl. 10, figs.11-14) from the British Lower and Middle Cenomanian is not considered conspecific with the nominative species, which should perhaps be renamed *P. phylloptera phylloptera* to distinguish Bosquet's original form from its subspecies. It should be noted that all references in the biostratigraphical section of this thesis to *P. phylloptera* are to the latter with the specific name shortened for the sake of brevity. The subspecies itself is slightly smaller, with a weak anterior marginal rib, no spines on the crest of the ventro-lateral ala..

Guernet (1990, p. 284, present author's translation) notes that "while the hinge cannot be distinguished, the species can easily be distinguished from others of the tuberculata group of *Pterygocythereis* by the existence of an oblique ridge which extends from the ocular tubercle in the direction of the centre of the valve. In the Maastrichtian, *P. phylloptera* gives rise to *Pterygocythereis kokeni* (Guernet, pl. 1, fig. 12) which can be distinguished by its smooth ventral margin and by the presence of a subcentral swelling." (Deroo, 1966).

Figure 2.5 shows the morphological characteristics of adult and late stage juveniles, adapted from Herrig (1965, fig. 80, p. 835) and annotated by the present author to show the main diagnostic features. One of the features of this species is its large, glassy eye tubercle, present in both adult and juvenile specimens; the alar process is also prominent in late stage juveniles. The dorsal spines also are characteristic; these curve backwards and the first spine behind the ocular tubercle is particularly strong. In the juvenile specimen, the first and second dorsal spines are prominent but the third postero-dorsal spine has yet to form. The anterior margin, ventral and posterior margins are spinose in adult specimens

but smooth in juveniles. In the present study, the majority of specimens were adults but late stage juveniles were also present, identifiable on the basis of the hinge and inner lamella. The ontogeny was not complete and very few earlier stage instars were evident.

Published range. *P. phylloptera*, from published records, is restricted to Northern Europe. Herrig, 1965, reports it in the Rügen Chalk of Germany, while Neale figured specimens from the Chalk of Northern Ireland. Jones & Hinde (1890) also record it from Northern Ireland and France. The published range is Campanian to Lower Maastrichtian in Britain, Holland and Poland (Neale, 1978).

Range in this study. Ranges in the outcrop samples from the Lower Campanian *G. quadrata* Zone (9), throughout the Upper Campanian. It does not appear in the Sidestrand assemblages but is present in the *O. lunata* Chalk and Grey Beds at Trimingham.

Pterygocythereis sp. 1.

Pl. 23, fig. 19.

Diagnosis. A small species with a clear eye tubercle and smooth margins.

Dimensions.	L	H
(MPK 11776)	0.60	0.26

Depository. MPK 11776

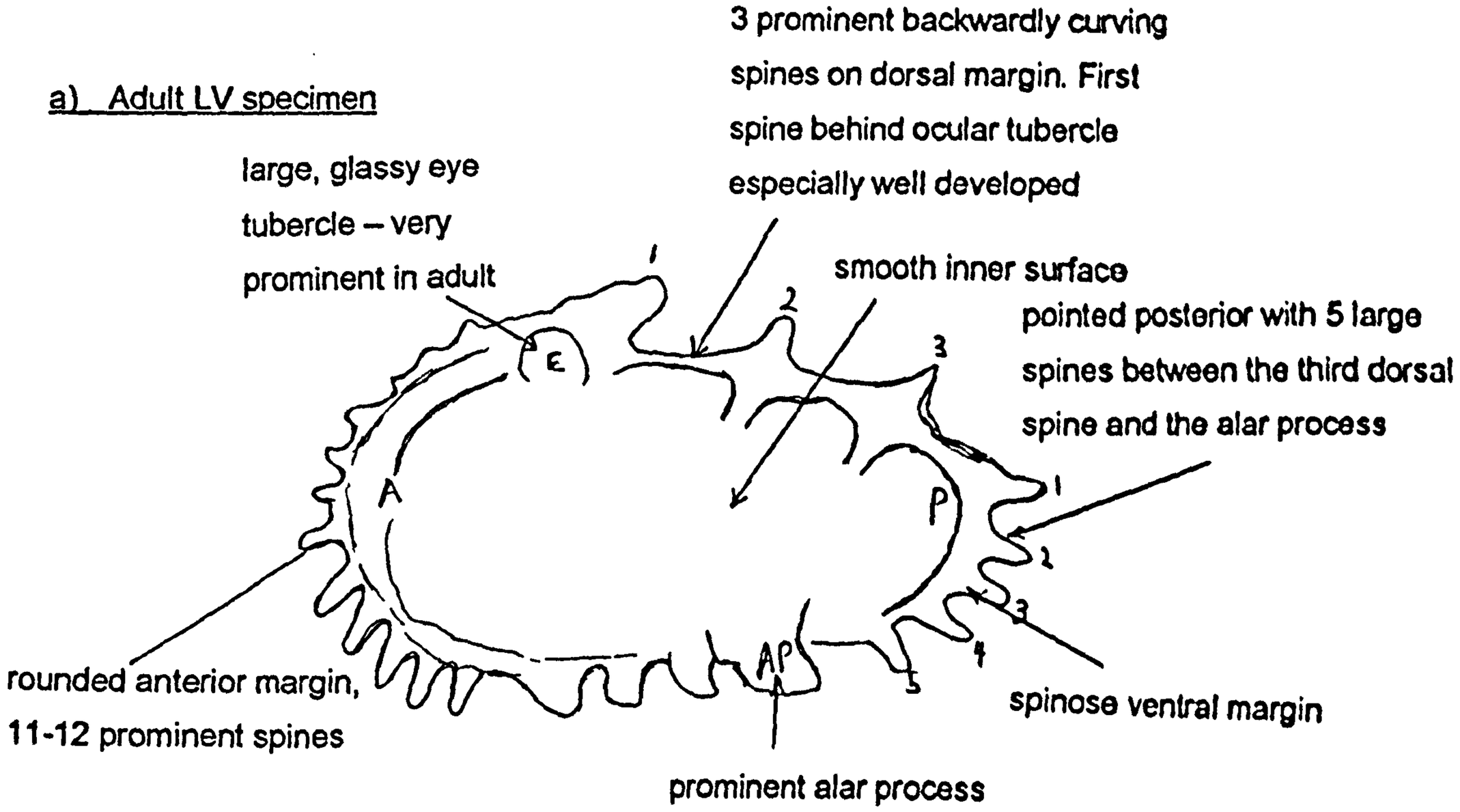
Material. 2 specimens.

Remarks. Left in open nomenclature due to its rarity; this species is slightly smaller than *P. phylloptera* and is closer to late stage juveniles of the latter. Its large, hemispherical, glassy eye tubercle mitigates against this, since in the late stage instars of *phylloptera*, the ocular tubercle is just beginning to be prominent. Adult specimens are considerably more spinose and the shell is less heavily calcified. In sp. 1, the valve is more robust and heavily calcified and the margins are non-spinose. It is possibly new but bears some resemblance to some species illustrated by Guernet and other authors.

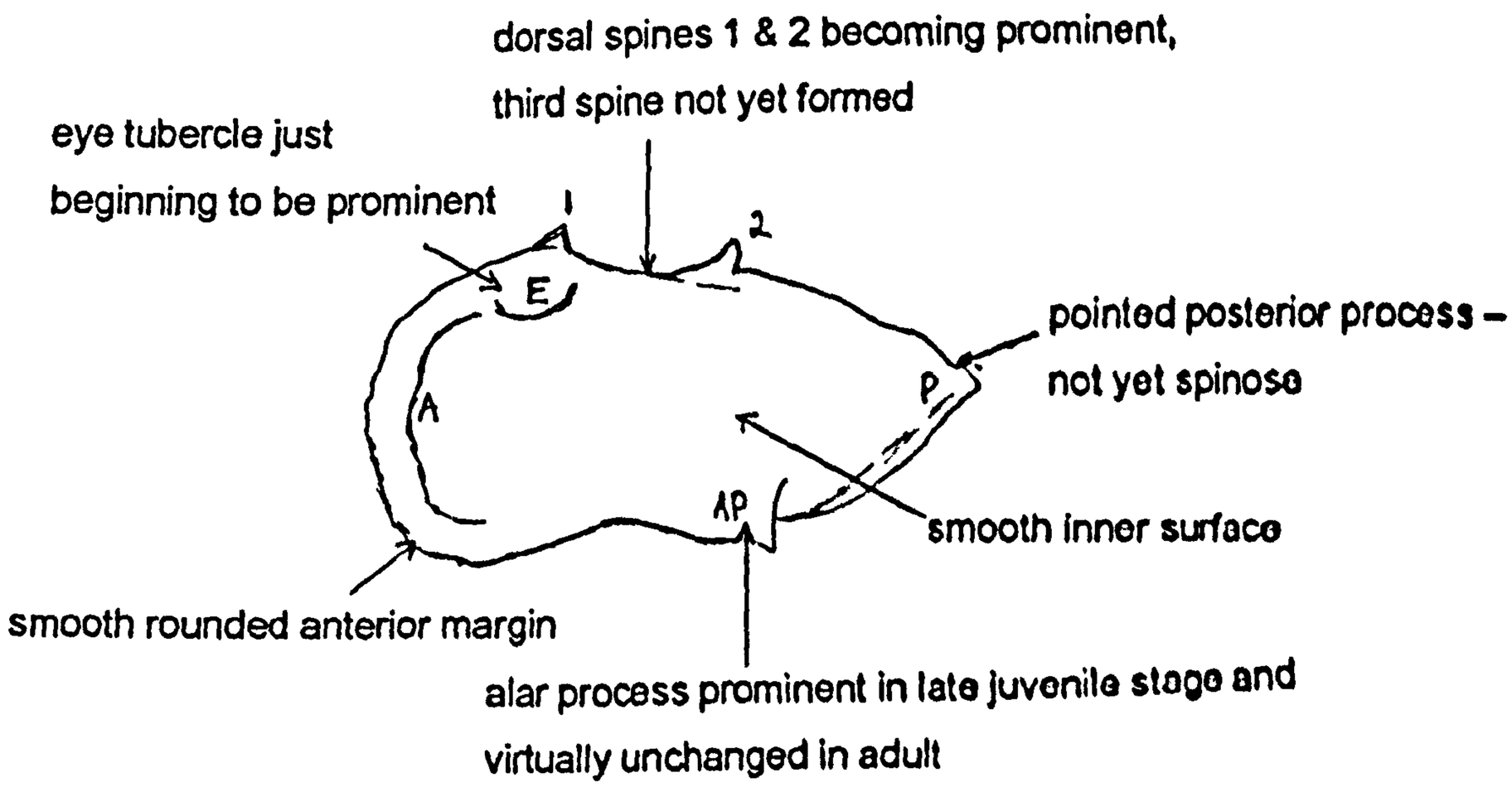
Range in this study. Restricted to the Upper Campanian Beeston Chalk and the Lower Maastrichtian pre-*Porosphaera* Beds.

Fig. 2. 5. Schematic drawings of a) adult and b) late-stage instar stages of *Pterygocythereis phylloptera* (Bosquet); adapted from Herrig (1965, text fig. 80, p. 835) and annotated to show the main morphological characteristics.

a) Adult LV specimen



b) Late stage juvenile specimen:



Genus TRACHYLEBERIDEA Bowen, 1953, emend. Haskins, 1963.

Treatise reference: Q 341

Treatise diagnosis: "Like *Costa* but posterior tooth of hinge tending to be lobate (hemiamphidont), antennal muscle scar broken into two, and median ridge of ornament discontinuous, dominated by subcentral tubercle, not bent at posterior end."

Taxonomic note. The above diagnosis is clearly inadequate and the generic range, given in the 1961 *Treatise* as Palaeocene to Oligocene can be extended. The genus is well known in the Upper Cretaceous of Northwest Europe and it has also been recorded from Recent sediments. It is discussed from a palaeoecological viewpoint in chapter 4 of this thesis. Babinot, 1980, also discusses the genus in more detail. The following characteristics are diagnostic in the genus *Trachyleberidea:*

1) Shape typically triangular, elongate; anterior margin broadly rounded.

2) Carapace strongly laterally compressed.

3) Ornament variable; reticulate in open marine environments, typically trefoil celation alters with increasing depth. Shelf species show a simple, open pattern of reticulation.

4) Median ridge weakly developed or absent in post-Cretaceous species.

5) Subcentral tubercle absent or weakly developed, more obvious since the Upper Cretaceous.

6) Eye tubercle generally prominent in Upper Cretaceous species; weak or absent in younger species.

King, 1968, MS, (p. 255), writes that *T. acutiloba* and *T. geinitzi* "were included by most recent workers in the genus *Cythereis* until 1964, when Pokorny erected the new genus *Spinicythereis* with *Cythere geinitzi* as the type species. At the same time, Haskins (1963) and Hazel (1965) emended the obscurely diagnosed genus *Trachyleberidea* so that these forms fall within its emended diagnosis. *Spinicythereis* must now be regarded as a junior synonym of the latter genus."

Trachyleberidea acutiloba (Marsson, 1880)

Pl. 24, figs 8-16, 18.

1880 *Cythere acutiloba* Marsson, p. 42, pl. 3, fig. 11.

1890 *Cythereis spinicaudata* Jones & Hinde, p. 28, pl. 2, figs 17-18

1940 *Cythereis acutiloba* (Marsson). Bonnema, p. 132, pl. 4, figs 59-66.

1958 *Cythereis acutiloba* (Marsson). Howe & Laurencich, p. 179.

1964a *Trachyleberidea acutiloba* (Marsson). Kaye, pl. 8, figs 7-8, 10.

1964 *Planileberis ? fastigata* Damotte, p. 106, pl. 1, fig. 8a-e; pl. 2, figs 13a-c.

1965 *Planileberis acutiloba* (Marsson). Szczechura, p. 536, pl. 3, figs 4-5; pl. 17, figs 1-3.

1965 *Planileberis ? fastigata* (Marsson). Damotte, pl. 4, figs 33, 34.

1966 *Trachyleberidea acutiloba* (Marsson). Herrig, p. 824, pl. 17, figs 3-6.

1966 *Planileberis? acutiloba* (Marsson). Deroo, p. 163, pl. 25, figs 798-200.

1968 *Trachyleberidea geinitzi* (Reuss). King, MS, pl. 28, figs 1-5.

1968 *Trachyleberidea acutiloba* (Marsson). Gründel, p. 43, pl. 2, figs 13-15.

1970 *Trachyleberidea* cf. *acutiloba* (Marsson). Donze *et al.*, pl. 13, fig. 17.

1971a *Trachyleberidea acutiloba acutiloba* (Marsson). Damotte, pl. 6, fig. 6, text fig. 14B.

1971a *Trachyleberidea acutiloba fastigata* (Damotte). Damotte, pl. 6, fig. 7, text fig. 14C.

1978 *Trachyleberidea geinitzi* (Reuss). Neale, p. 362, pl. 15, figs 5-9.

1979 *Trachyleberidea acutiloba* (Marsson). Babinot & Colin, pl. 1, figs 3-7.

non 1980 *Trachyleberidea acutiloba* (Marsson). Babinot, pl. 27, figs 1, 2.

1983 *Trachyleberidea geinitzi* (Reuss). Babinot *et al.*, 1983,

Diagnosis. A small to medium species of *Trachyleberidea* with strongly convergent dorsal and ventral margins with a slight posterior spine; strongly reticulate with weak ventral and anterior marginal ribs and a low subcentral tubercle. Sexually dimorphic; males more elongate and less inflated than females.

Dimensions.	L	H
RV female (MPK 11782)	0.63	0.33
LV male (MPK 11783)	0.67	0.32
LV female (MPK 11790)	0.66	0.34
RV male (MPK 11784)	0.68	0.32
RV female (MPK 11788)	0.65	0.33

Depository. MPK 11782-11792.

Material. More than 100 specimens.

Remarks. Kaye, 1964a, figured Jones & Hinde's specimen of *C. spinicaudata* which he considered to be conspecific with Marsson's *Cythere acutiloba* and Bonnema's *Cythereis acutiloba* (Marsson), writing (p. 70) that "the shape and internal features of the species, however, fall within Haskin's (1963) redefinition of the genus *Trachyleberidea.*" The present author is in agreement and included the former in synonymy.

King, 1968, MS, illustrates specimens attributed to *T. geinitzi* which are identical to the present material and that figured by Damotte, 1971, and other authors. They are, therefore, included in the present synonymy as conspecific with *T. acutiloba,* as are the specimens illustrated by Neale, 1978, from the Upper Chalk of Sonning, Berkshire. The specimens in the latter study, are, however, slightly larger than the present material (measured specimens 0.69mm in length). Neale (p. 362) states that " often referred to as *T. acutiloba* (Marsson, 1880), this is now considered to be a junior synonym of *T. geinitzi.*" Many other authors do not agree and Babinot & Colin, 1979, consider the two as separate species belonging to the first of four main morphological groups of the genus in the Upper Cretaceous. Where *T. geinitzi* is referred to in the synonymy, the illustrated specimens are considered to be conspecific with *T. acutiloba.* The two species have been confused during their history and work is needed to separate their confused synonymies. This will not, however, be attempted here.

Damotte describes two subspecies from the Campanian of the Paris Basin: *Trachyleberidea acutiloba acutiloba* and *T. acutiloba fastigata.* Both subspecies are included in synonymy with Marsson's species; they are separated on minor size differences (subspecies *acutiloba* - 0.58-0.64mm in length; subspecies *fastigata* - 0.55-0.58 mm). The former has a broader anterior margin and the sub-central tubercle is more prominent. They could represent adults and late-stage juveniles of the same species but the hingement in both subspecies is adult (Damotte, 1971a, p. 96, text figs 14B and 14C) and, when the

ranges are compared, certain trends are evident. The former subspecies occurs in the Upper Campanian of the Paris Basin and the English Chalk (*mucronata* Zone) and in the Upper Campanian - Lower Maastrichtian of Belgium and Poland. The latter occurs in the Upper Santonian and Lower Campanian of the Paris Basin and England. The present material is closer in size and ornament to *T. acutiloba acutiloba* and, in the range charts (vol. 2, chapter 3) all specimens are referred to *T. acutiloba*.

Donze *et al.*, 1970, illustrate *T.* cf. *acutiloba*. The only apparent difference between this form and the species as it appears in the present study is the less prominent sub-central tubercle; this may be due to a certain degree of morphological variability, preservation or the illustration of a sub-adult specimen.

The specimen figured by Babinot, 1980, is very different from *T. acutiloba* of other authors and is clearly not conspecific. There is no evidence of reticulate ornament and the surface is pustulose. It is closer to *Trachyleberidea pokornyi* King, 1968, MS (pl. 28, figs 6, 7, 9), from the Upper Campanian of Norfolk, to which *Trachyleberidea* sp. in the present study has been compared.

Published stratigraphical range. In a study of selected ostracod species from the British Upper Chalk, King, MS, notes that the species shows "an extremely wide stratigraphical and geographical distribution" It ranges from the *coranguinum* Zone to the Lower Maastrichtian in Europe and is common in both the Northern and Mediterranean provinces. It is restricted to the Campanian to Maastrichtian according to Herrig, 1966, and Deroo, 1966, but Gründel, 1968, records it from the German Santonian; Damotte, 1971a reports it from the Upper Campanian of the Paris Basin and the English Chalk (*B. mucronata* Zone) and in the Upper Campanian to Lower Maastrichtian of Belgium and Poland (*T. acutiloba acutiloba)* but also illustrates a second subspecies (*T. acutiloba fastigata)* from the Upper Santonian and Lower Campanian of the Paris Basin and England. Babinot *et al.*, 1972, illustrate *Trachyleberidea* gr. *acutiloba* from the French Middle Turonian to Middle Cenomanian, but this is not considered conspecific. A recent zonation of various British Upper Cretaceous species adapted from Neale, 1978 (table 5, p. 377) and other authors record it from the Coniacian.

Range in this study. In the outcrop samples, this species ranges from the Coniacian -?- Lower Campanian to Lower Maastrichtian. It first appears in the Coniacian *coranguinum* Zone (zone 3) at South Pickenham and Litcham. It is a Lazarus taxa across the Santonian and most of the Lower Campanian in Norfolk and Suffolk, reappearing again in the Lower Campanian *Gonioteuthis quadrata* Zone (9). It is significantly more abundant in the Upper Campanian and Lower Maastrichtian. In the Upper Campanian, it occurs in the basal *mucronata,* Eaton, Weybourne, Beeston and Paramoudra chalks (10-14) at various localities. In the Lower Maastrichtian, *T. acutiloba* occurs in the pre-*Porosphaera* and *Porosphaera* Beds at Sidestrand (15, 16) and the *O. lunata* Chalk of Trimingham (17). It was not seen in the overlying Grey Bed samples. The species is also present in samples from the Santonian high *coranguinum* Zone (SAG 2057 - Witham Borehole; SAG 2058 - Kelvedon Borehole) in Essex. This occurrence is not included in the stratigraphical range charts (volume 2, chapter 3), which are drawn only for Suffolk and Norfolk.

In the Trunch Borehole, the species first appears in the Lower Campanian, throughout the *O. pilula* Zone (7; FAD SAG 616) and in the upper part of the *G. quadrata* Zone (9). It is a Lazarus species in the basal *mucronata* Chalk, reappearing in the basal sample of the Eaton/Weybourne Chalk (11/12); it is a regular component in the assemblages of the Beeston and Paramoudra chalks (13, 14). It is present

in the Lower Maastrichtian *Porosphaera* Beds (16) in SAG 216 and 213, with a Lazarus absence in the underlying pre-*Porosphaera* Beds.

Trachyleberidea vezerae Colin, 1973.

Pl. 24, figs 17, 21-23.

1973 *Trachyleberidea vezerae* Colin, pl. 63, figs 6-7.

1985 *Trachyleberidea vezerae* Colin. Babinot *et al.*, p. 240; pl. 63, figs 6, 7.

Diagnosis. A large species of *Trachyleberidea* with a dentate antero-marginal flange, a strong antero-marginal rib behind which is a fan-shaped array of some 8 hexagonal fossae. Ornament consists of regular hexagonal reticulations which cover the entire lateral surface. Postero-dorsal loop bispinose. Sub-central tubercle large, low and smooth.

Dimensions.	L	H
LV (MPK 11791)	0.72	0.34
LV (MPK 11795)	0.71	0.33
RV (MPK 11796)	0.72	0.34
juv. RV (SAG 105)	0.60	0.28

Material. More than 60 specimens.

Remarks. The present material is identical to Colin's figured specimens and the holotype and topotype illustrated by Babinot *et al.*, 1985. Babinot *et al.*, also illustrate *Trachyleberidea arta* (Damotte, 1971) from the French Middle and Upper Cenomanian. This species is variable; it is similar in shape to the present material but differs in its ornament. One specimen (pl. 65, fig. 1) has a reticulate ornament with the fossa appearing celate as in *T. vezerae*, but the posterior is narrower, with a large ventro-lateral process. The ornament is more regular. The second specimen (pl. 65, fig. 2) is non-reticulate and its entire lateral surface is covered with very small raised pustules. It is unlikely that the two are conspecific.

Published stratigraphical range. Colin, 1973, and Babinot *et al.*, 1985, illustrated this species from the Upper Turonian of France. The present material should, perhaps, be designated *T.* cf. *T. vezerae* to reflect the difference in age, but the specimens of this study are very close to Colin's type material.

Range in this study. Restricted to the Upper Campanian and Lower Maastrichtian. In the outcrop samples, it occurs in the basal *mucronata* Chalk at Eaton and Cringleford and the Middle Weybourne Chalk at Keswick. It is rare in the pre-*Porosphaera* and *Porosphaera* Beds and the *O. lunata* Chalk. In the Trunch Borehole, it first appears in the basal Eaton/Weybourne Chalk (SAG 404) and sporadically in the Beeston and Paramoudra chalks. It extends to SAG 213 (Lower Maastrichtian *Porosphaera* Beds).

Trachyleberidea sp.

Pl. 24, figs 19, 20

Diagnosis. A medium, fairly compressed species; anterior margin broadly rounded with small, prominent eye tubercle and a clear marginal ridge. Posterior margin narrow; dorsal margin straight, converging with slightly concave ventral margin. Small subcentral tubercle in some specimens; very faint median rib and

weak ventro-lateral rib. Primary ornament covers entire lateral surface - a regular reticulate network of small polygonal fossa; each fossa with secondary ornament.

Dimensions.	L	H
LV (MPK 11793)	0.68	0.31

Material. 3 specimens.

Remarks. This species may possibly be compared to *T. pokornyi* King, 1968, MS (pl. 28, figs 6, 7, 9), from the Upper Campanian of Norfolk, but is left in open nomenclature due to its rarity and the fact that King's species is unpublished. The ornament is less spongy and more reticulate. It differs from *T. acutiloba* in its larger size and less open reticulate ornament in which the fossa are significantly smaller than in the former species. *Trachyleberidea vezerae* Colin, which also appears in the present study, is similar in shape but lacks the marginal denticles. In *T. vezerae*, the ornament is reticulate with large, regular fossa. In *T.* sp., the fossa are smaller and almost polygonal with secondary features.

Range in this study. This species is rare and is represented by one specimen from the Upper Campanian Middle Weybourne Chalk of Keswick (SAG 105) and two specimens from the middle of the Lower Campanian *Gonioteuthis quadrata* Zone (SAG 466) of the Trunch Borehole.

UNDETERMINED GENERA:

Gen. et indet. sp. 1.

Pl. 26, fig. 7

Diagnosis. An elongate specimen with a broadly rounded, denticulate anterior margin and a small, spherical eye tubercle. Anterior part of valve flattened with a reduced ornament. Valve widens in front of large subcentral tubercle with two rounded tubercles; dorsal margin straight, spinose with a large postero-dorsal spine. Ventral margin convex, straight behind subcentral tubercle with a similarly sized postero-ventral spine and a smaller tubercle equidistant between the two. Posterior narrow, spinose. Ornament behind sub-central tubercle consists of round pits which are larger on the posterior part of the valve; pitting finer and more closely spaced in front of the sub-central tubercle. Hinge structure obscured.

Depository. MPK 11796

Dimensions.	L	H
LV (?male) (MPK 11796)	0.65	0.27

Material. A single specimen.

Remarks. This individual does not conform to any known Cretaceous species. It is possibly new, but is left in open nomenclature due to its rarity and uncertain taxonomy. It could be a late-stage juvenile of a larger species not seen in this study in its adult form. Although genus and species cannot be determined; the present author would assign it to Trachyleberididae, subfamily Trachyleberidinae, on the basis of its size, shape and clear subcentral tubercle. The spinose nature of this last feature may place it in *Cythereis* and exclude it from *Rehacythereis*. It is similar in shape to *Cythereis wrightii* Jones & Hinde from the "Chalk" of Northern Ireland, but this is larger and less elongate; the posterior is sharply pointed and the lateral surface is smooth.

Range in this study. Restricted to the Lower Maastrichtian, this species was found in a single sample (SAG 2007) from the Grey Beds of Trimingham.

Gen. et indet. sp. 2

Pl. 26, figs 1

Diagnosis. An elongate trachyleberid with a prominent eye tubercle and small hinge ear. Anterior margin rounded, spinose; dorsal and ventral margins straight, sloping to narrow posterior. Ornament reticulate.

Dimensions.	L	H
LV (MPK 11797)	0.68	0.27

Material. 1 specimen.

Remarks. This specimen was, therefore, left in open nomenclature due to its rarity and uncertain taxonomic position. It could belong to *Cythereis* or *Rehacythereis* based on its shape and ornament. It has a clear eye tubercle but the sub-central tubercle is absent or obscured.

Range in this study. In the outcrop samples, this species is restricted to the Lower Maastrichtian *O. lunata* Chalk of Trimingham, where it occurs in a single sample (SAG 2001).

Gen. et indet. sp. 3

Pl. 26, fig. 2, 8

Diagnosis. A medium, rather tumid trachyleberid species. Anterior margin broadly rounded; dorsal margin straight with short postero-ventral spine; ventral margin rounded with slight ventro-lateral rib which is obscured by ornament in one of the specimens. Posterior spinose, narrow and downwardly curved. Greatest height at mid-point; large sub-central tubercle. Ornament variable; strongly reticulate across more than two-thirds of the valve.

Dimensions.	L	H
RV (MPK 11799)	0.60	0.31

Depository. MPK 11798, 11799

Material. 2 specimens.

Remarks. One of the specimens appears abraded and the other has an open reticulate network. Both show the same shape and tumidity, with a narrow, downwardly curving posterior and a distinct ventro-lateral rib. They could be accommodated in *Mosaeleberis* but also several other genera. The specimens are left in open nomenclature due to their rarity and uncertain taxonomic position.

Range in this study. Upper Campanian Paramoudra Chalk, Trunch Borehole; (SAG 277).

Gen. et indet. sp. 4

Pl. 26, fig. 3.

Diagnosis. A small, triangular specimen with a broadly rounded anterior margin. Narrow anterior rib joins a distinct ventrolateral rib; dorsal and ventral margins straight, sloping to narrow flattened posterior. Large postero-dorsal tubercle. Ornament reticulate across entire lateral surface, reduced on posterior.

Dimensions.	L	H
LV (MPK 11800)	0.46	0.21

Depository. MPK 11800

Material. 1 specimen.

Remarks. This specimen is distinctive but cannot be readily attributed to any genus or species in this study. It is, therefore, left in open nomenclature. It is similar to a species in this study tentatively assigned to ?*Nipponocythere* in its shape, flattened valves and ventro-lateral rib but differs in its reticulate ornament. The latter is clearly punctate.

Range in this study. A Lower Maastrichtian sample (SAG 1) from the site of the Overstrand Hotel.

Gen et indet. sp. 5.

Pl. 26, fig. 4, 5

Diagnosis. A broken specimen; rounded anterior margin with 16 short spines; dorsal and ventral margins straight; posterior not seen. Sub-central tubercle obscured by reticulate ornament. Ornament consists of irregular, celate fossa with several small tubercles.

Dimensions.	L	H	
LV (MPK 11801)	0.70	0.39	(specimen broken)

Material. 2 specimens.

Remarks. This species belongs to either *Cythereis* or *Rehacythereis* but is left in open nomenclature due to its rarity and uncertain taxonomic position.

Range in this study. Lower Campanian *Gonioteuthis quadrata* Zone, Trunch Borehole (SAG 544, 449).

Gen et indet. sp. 6.

Pl. 26, fig. 6

Diagnosis. A small, triangular species with a clear eye tubercle, a broadly rounded anterior margin and a narrow, rounded posterior. Dorsal and ventral margins straight with two short postero-dorsal spines. Ornament rather indistinct, reticulate with two large, rounded tubercles on the anterior part of the valve.

Dimensions.	L	H
LV (MPK 11802)	0.33	0.18

Material. A single specimen.

Remarks. This specimen is rather like *Eucytherura dorsotuberculata* in size and shape. It differs, however, in the positioning of the tubercles. In the latter species, these are situated along the dorsal margin. In the present specimen, there are two large, rounded tubercles on the anterior part of the valve. The eye tubercle is smaller and there are two postero-dorsal spines

Range in this study. SAG 217, Lower Maastrichtian pre-*Porosphaera* Bed of the Trunch Borehole.

Genus PHACORHABDOTUS Howe & Laurencich, 1958

Original description of genus. Howe & Laurencich, 1958, p. 456 "A genus of Trachyleberinae with smooth, ovate, lenticular, somewhat laterally compressed carapace; dorsal, median and ventral ribs appear as raised lines. The upper margin nearly straight; the ventral rib incurved near the middle, the two converging towards the back. Anterior broadly rounded, with a thin fragile frill, but with no marginal ridge." (see remarks) "Posterior narrowly rounded in left, sub-angular near middle in right. Eye spot present but indistinct. Muscle swelling on outside and represented by a deep pit on inside, its surface being nearly covered by the closing and mandibular scars, whose arrangement is difficult to see because of the curvature of the pit. Hinge holamphidont. Marginal area very broad on the thin compressed anterior end; the long radial canals tending to occur in pairs."

Treatise reference. Q 339

Treatise diagnosis. "Hinge holamphidont. Like *Costa*, but less elongate, smoother, with ribs less well developed, sub-central tubercle wider, and wider duplicature. Eye tubercle present but indistinct."

Remarks. Howe & Laurencich (1958, p. 456) note that " described species referred by us to this genus have previously been referred to *Cythereis*. Externally, they do not have the shape of *Cythereis*; they lack a surface reticulation and the ventral side is definitely less flattened. Internally, the hinge lacks crenulation on the terminal teeth and the marginal area is much wider than in *Cythereis*".

Species of *Phacorhabdotus* have been described by other authors post-Howe & Laurencich (e.g., *P. batavus* Deroo, 1966 and others) with clear marginal ridges. The type description for this genus should be extended to include forms with such a feature.

A similar genus *Imhotepia* was erected by Pokorny in 1964, distinguished by its anterior rib, ornamented surface and its paramphidont to holamphidont hinge. Weaver (1982, p. 71, pl. 14, figs 1-4) illustrates *Imhotepia euglyphea* from the Plenus Marl. *Phacorhabdotus* has a holamphidont hinge and anterior rib in some species, but is more weakly ornamented. Gründel (1974c, p. 106) places both genera within the tribe Phacorhabdotini that can, with some probability, be traced back to Lower Cretaceous representatives. Within the tribe, there are several "phylogenetic trends" comprising in part the whole tribe, in part some portions of it. Most important are "loss of the eye tubercle, reduction of the sculpture, widening of the calcified inner lamella and the development of an irregular internal rim, as well as the formation of forked or branched radial pore canals."

Hazel & Paulson, 1964, discuss some apparent phylomorphogenic trends in the Austinian and Tayloran (Coniacian and Campanian) of Texas. They describe several "primitive" *Phacorhabdotus* species. *P. semiplicata* Reuss of Alexander, 1929, is, in this later work described as *P. pokornyi*, which differs from other known examples at the time of publication in having an eye tubercle and, by being denticulate around its anterior margin. The species also has a strong marginal rim. The eye tubercle and denticulations were considered by Hazel & Paulson to be "primitive characters that are later lost", but this is probably due to the authors following Howe & Laurencich's original type descriptions. This makes no mention of the marginal rib

found in many other species. The presence of eye tubercles and marginal ribs and denticles are not always, in the opinion of the present author, primitive characteristics but the inevitable consequence of other authors increasing the number of species belonging to the genus since its original conception. Hazel & Paulson (p. 1051) make the point that the reduction or loss of the anterior marginal rib does not seem to be a consistent trend throughout the genus. *Phacorhabdotus lonsdaleianus* (Jones), in the present study, would seem to be more morphologically advanced than *P. pokornyi*.

Pokorny (1963) studied the genus in the Upper Cretaceous of Czechoslovakia and traced the phylogenetic lines of *Phacorhabdotus marssoni* Bonnema, 1940. He noted several phylomorphogenic trends, i.e. widening of the zone of concrescence and the reduction in sculpture, with an extensive revision of *Cytherina semiplicata* Reuss, 1846, showing that the latter is *Phacorhabdotus* (1963, p. 69). Pokorny also makes additions to the original generic diagnosis regarding such features as hinge structure, anterior marginal rib, eye tubercle, radial pore canals and muscle scars. The present author agrees with all these revisions, except one. Firstly, the hinge may be holamphidont but also hemiamphidont, the former originating from the latter by loss of crenulation (Pokorny's "notches") on the posterior tooth (see Pokorny, 1963, p. 79 for discussion). Secondly, the anterior marginal ridge may be considerably raised, as in *P. lonsdaleianus* in the present study, or absent, as in the type species *Phacorhabdotus texanus* Howe & Laurencich, 1958, and *P.* ex. gr. *semiplicatus* described by Pokorny from the Coniacian of Czechoslovakia. The present author agrees with Pokorny, 1963, and other authors (e.g. Hazel & Paulson, 1964; Pietrzeniuk, 1965; Gründel, 1974) in that the presence or absence of the marginal ridge seems to have little taxonomic importance in this group. Pokorny considers the absence of the ocular tubercle to be a "secondary feature, connected with the general reduction in sculpture." However, the same author finds no eye tubercle (based on *P. semiplicatus* and *P. texanus).* The current author agrees with the *Treatise* diagnosis; some species have clear eye tubercles, while in others, this feature is absent. Radial pore canals and muscle scar configuration will not be discussed, since these features are not seen in the present material.

Pieterzeniuk (1965) discussed problems associated with the phylogenetic evolution of *Phacorhabdotus*, based on two species from the German Palaeogene, but also discusses several Cretaceous representatives with special reference to muscle scar formation (p. 1106-7; see also Gründel, 1974c, p. 103).

Phacorhabdotus leiodermatos sp. nov.

Pl. 25, figs 16, 18-20.

Derivatio nominis. Gr. λειοδρματοζ - bald, smooth skinned, from the smooth intercostal lateral surface of this species.

Holotype, LV male (MPK 11629)

Type level, SAG 109, Upper Campanian, Beeston Chalk.

Type locality, Cringleford, Norfolk.

Diagnosis. A medium to large species of *Phacorhabdotus* characterized by its smooth surface and extremely broad anterior margin; eye tubercle small and indistinct. Dorsal margin straight with two short oblique ribs;

ventral margin straight, obscured by low ventral ridge. Subcentral tubercle small and slightly elongate. Short, weakly developed median rib extends back to a similarly sized posterior tubercle. posterior narrow, spinose.

Description. Medium to large. Subquadrate in lateral view, fusiform in dorsal view of the complete carapace; anterior margin broadly rounded with a distinct marginal rim; apex at about mid-height. Narrow spinose posterior, apex at about mid-height. Eye tubercle indistinct, very small and spherical. Dorsal margin straight with two faint, very short oblique ribs; ventral margin straight, obscured by low ventral ridge; small, slightly elongate sub-central tubercle, highest point corresponding to position of sub-central tubercle. Short faint median rib behind central tubercle. Lateral surface smooth and featureless, shell material heavily calcified. Sexual dimorphism, males more elongate than females. LV anterior margin more broadly rounded, slightly larger than RV. Juveniles absent.

Marginal area moderately broad at anterior, narrower at posterior; hinge indistinct; other internal details obscured.

Dimensions.	L	H
Holotype LV male, (MPK 11629)	0.73	0.34
Paratype LV female, (MPK 11630)	0.67	0.37
Paratype RV female, (MPK 11632)	0.65	0.36
Paratype female C (MPK 11631)	0.67	0.37

Depository. MPK 11629-11632

Material. 11 specimens

Remarks. This species is rather distinctive. It shares the anterior rib and oblique dorsal ribs of such species as *P. semiplicatus* and *P. lonsdaleianus* but is much larger and the lateral surface is smooth and more heavily calcified. The sub-central tubercle is smaller and less prominent. In both the aforementioned species, this feature is hemispherical but in the present material, the sub-central tubercle is slightly elongate, with a short median rib and similar sized posterior tubercle. The posterior margin is more spinose. *Phacorhabdotus batavus* Deroo, 1966, is much smaller (recorded by Damotte, 1971a, p. 83, pl. 4, fig. 17 as 0.49-0.52 mm in length), with a wide anterior marginal rib and a narrowly rounded posterior; both dorsal and ventral margins straight, sloping obliquely to the posterior. It is a smooth species with a marginal ridge, but the sub-central tubercle is not evident and it lacks the short oblique dorsal ribs and posterior tubercle of the present species. *Phacorhabdotus strangulans* Damotte, 1971a, (p. 83, pl. 4, fig. 17) has a smooth lateral surface but is much smaller, with lengths ranging from 0. 49 to 0.52 mm, with a wide anterior marginal rim and a narrowly rounded posterior; both dorsal and ventral margins straight, sloping obliquely to the posterior. *P. strangulans* does not, however, have the two short oblique dorsal ribs.

Range within this study. Restricted to the Upper Campanian basal *mucronata* Chalk, Beeston Chalk and lower levels of the Paramoudra Chalk at Cringleford and Whitlingham respectively; this is an extremely rare species which was not found in the Trunch Borehole.

Phacorhabdotus lonsdaleianus (Jones, 1849)

Pl. 25, figs 1-12, 14.

1849 *Cythere (Cythereis) lonsdalieana* Jones, p. 20, pl. 5, fig 20a-b

1870 *Cythere lonsdaleiana* Jones, p. 75, 76.

1880 *Cythereis fillicosta* Marsson, pl. 3, fig. 12a, b.

1890 *Cythereis lonsdaleiana* Jones. Jones & Hinde, p. 1, fig. 64, 65, *non* fig. 40-42, 66.

1936 *Cytheridella lienenklausi* Veen, pl. 9, fig. 8-9 = *Archicythereis lienenklausi* Veen, amend. p. 163.

1940 *Archicythereis lienenklausi* Veen. Bonnema, pl. 4, figs 21, 22.

1941 *Cythereis fillicosta* Marsson. Bonnema, pl. 4, figs 48 - 53.

1958 *Cythereis lonsdaleiana* Jones. Howe & Laurencich, p. 209-10.

1958 *Cythereis fillicosta* Marsson. Howe & Laurencich, p. 198.

1958 *Archicythereis lienenklausi* Veen. Howe & Laurencich, p. 55.

1964 *Cythereis lonsdaleiana* Jones. Kaye, p. 63, pl. 7, figs 7, 10.

1965 *Phacorhabdotus fillicosta* form a (Marsson). Damotte, pl. 6, fig. 28.

1966 *Phacorhabdotus londsdaleianus* (Jones) Herrig, pp 825-831, pl. 19, figs 4-8, text figs 74-77

1968 *Pseudophacorhabdotus lonsdaleianus* (Jones). King, MS, pl. 25, fig. 8; pl. 26, figs 1, 2, 4, 5.

1978 *Phacorhabdotus lonsdaleianus* (Jones). Neale, pl. 15, fig. 10.

Diagnosis. A medium species of *Phacorhabdotus* with two short oblique dorsal ribs, an anterior marginal rib and a short median rib which extends across the posterior of the valve from the prominent, hemispherical sub-central tubercle. Anterior margin broadly rounded; dorsal and ventral margins nearly straight, converging towards the sub-acute posterior. Eye tubercle small but distinct. Hinge holamphidont.

Dimensions.	L	H
LV female (MPK 11615)	0.61	0.39
LV female (MPK 11617)	0.60	0.39
LV male (MPK 11616)	0.64	0.36
RV female (MPK 11621)	0.62	0.34
juv. (SAG 77)	0.53	0.30
juv. (SAG 53)	0.53	0.31

Depository. MPK 11615-11625.

Material. Nearly 300 specimens.

Remarks. Jones first described this species as a rare component of the Chalk of Norwich. Jones' illustrated specimens (pl. 15, figs a-c) are essentially identical to those of Neale, 1978. The material of the present study is also identical. Neale illustrates a RV that is identical to right valves from the Trunch Borehole and various outcrop localities in Norfolk and Suffolk. The adult specimens of the present study range from 0.60 to 0.60 to 0.65 mm in length; Neale's specimen is only 0.59mm. Herrig, 1965, however, gives a size range of 0.58-0.65mm. It is, therefore, a rather variable species. King, 1968, MS, (P. 237) notes a steady increase in the average length of LV specimens (1 specimen in the Lower Campanian *Gonioteuthis* Zone – 0.50 mm;

Upper Campanian basal *mucronata* Chalk - 0.52mm, Eaton Chalk - 0.58 mm, Weybourne Chalk - 0.59 mm, Beeston Chalk - 0.63 mm; Lower Maastrichtian *Porosphaera* Beds - 0.63 mm, White Chalk - 0.62 mm, 2 specimens in the Sponge Beds - 0.65mm). Although the majority of these measurements fall within the published range for this species, the two earlier instances (0.50 and 0.52 mm) probably represent juvenile individuals.

Chapman, 1898 (p. 341) listed the species as present in the Cambridge Greensand, but since this is not illustrated, this record is not included in synonymy. Herrig, 1967 records a subspecies, *P. lonsdaleianus retunsus* from the Upper Santonian to Upper Campanian of Northeastern Germany (pl. 1, text fig. 16, pl. 2, figs 4-5. This differs from the nominative species in that it has a slightly more convex anterior marginal rib and the eye tubercle is absent. The ventral rib, concave in *P. lonsdaleianus*, is longer and straight in the sub-form.

Van Veen (1936) describes *Cytheridella lienenklausi* from the Maastrichtian of South Limburg, later assigned to the genus *Archicythereis* Howe, 1936, which should, in the opinion of Howe & Laurencich, be regarded as "uncertain" .The description was based on a single damaged individual which is probably juvenile. Herrig, 1965, notes that the species is identical to larval forms of *P. lonsdaleianus* (p. 830). In the present synonymy, Veen's species is included as a junior synonym. Llebau (1975, p. 362) considers *Archicythereis* to be a valid genus, although misunderstood as a "taxonomic dustbin for trachyleberoid larvae for many years." Most authors, however, follow the assumption that it is synonymous with *Phacorhabdotus. Cythereis filicosta,* as figured by Bonnema and Howe & Laurencich, shows two clear oblique dorsal ribs and is identical to *P. londaleianus.* The present author has examined all records of the former species and is satisfied that it is conspecific with the latter (see also Herrig, 1966, pp. 825-831). It is, therefore, included in synonymy. King, 1968, MS, places *P. lonsdaleianus* in a new genus *Pseudophacorhabdotus,* but since this work is unpublished and the specimens appear conspecific with Jones' original material, the species is retained in *Phacorhabdotus.*

A similar species, *Phacorhabdotus semiplicata* appears as a very rare component in the present study in the Upper Campanian Beeston Chalk of the Trunch Borehole. It can be distinguished from *P. lonsdaleianus* by its smaller size and less distinct eye tubercle. Kaye, 1964a (p. 64) notes that "the multiple nature of the dorsal rib was the most diagnostic feature according to Bonnema who used this criterion for separating the form from *Cythereis semiplicata* (Reuss)." This species ranges from 0.45-0. 51 mm in its published length (see Pokorny, 1963c, text figures 1, 3, 6-14; pl. 1, figs 1, 2, 6); *P. lonsdaleianus* ranges in the present study from 0.63-0.67mm in length (Herrig's material was 0. 58-0. 65mm). The similarities between the two species, however, cannot be ignored and it is possible that they are related.

Published range. Jones, 1849, and Neale, 1978, both describe the species from the Norwich Chalk. In Britain, the published range is Upper Santonian to Lower Maastrichtian. King, 1968, MS, records the species from the Santonian *Marsupites* Zone to the Lower Maastrichtian, noting its abundance in the Upper Campanian and Lower Maastrichtian of Norfolk. Hart *et al.*, 1987, record it from the early to mid-Cenomanian of Whitecliff Bay, Isle of Wight, but since this is only in a list of species with no supporting illustrations so that this occurrence can probably be ignored. Herrig, 1965 (p. 831) gives a range of Upper Campanian to Upper Maastrichtian in the White Chalk of Germany and Northeastern Holland, and the

species is also recorded from the Lower Maastrichtian of Poland (Herrig, 1966, p. 830) and the Upper Maastrichtian of the Netherlands and Holland (Veen, 1936; Bonnema, 1940, 1941).

Range in this study. Conforms to the published range but also occurs in the highest *coranguinum* Zone in the Coniacian, representing a slight extension in the range of this species, i. e. Coniacian to Lower Maastrichtian. It occurs in almost all samples at South Pickenham and Litcham, Norfolk (Coniacian, SAG 113, 114, 115, 183, 184) and was also present in the assemblages of the Santonian high *coranguinum* Zone, but is absent in the *Uintacrinus* and *Marsupites* zones. It was also seen in the Santonian very high *coranguinum* Zone in a sample from the Kelvedon Borehole, Essex. It does not appear again in Norfolk until the highest samples of the Lower Campanian *pilula I* restricted *quadrata* Zone at Wells, and occurs in only two samples of the preceding restricted *quadrata* Zone. It is, however, significantly more abundant in the Upper Campanian and is present in almost all samples of the basal *mucronata* Zone, Eaton Chalk and Upper Weybourne Chalk at Eaton. It occurs in the upper samples at Catton Grove and is also present in all but one sample from the Beeston Chalk at Caistor-St-Edmunds. At Cringleford, the species occurs in the basal *mucronata* Zone Chalk, but is absent in the top sample and the overlying basal Eaton Chalk at this locality. It is almost ubiquitous in the Weybourne Chalk at Keswick and at Stoke Holy Cross. It is slightly more abundant in the Upper Campanian Paramoudra Chalk at Crown Point Pit and Church Pit, Whitlingham and also occurs in the Lower Maastrichtian pre-*Porosphaera* and *Porosphaera* Beds of Sidestrand (3.2% of assemblage in SAG 2017). It is less common in the *O. lunata* Chalk and Grey Beds of Trimingham (0.7-2.6%, 1.7% respectively). It occurs in 13 of the 18 zones studied (zones 3, 4, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18).

Phacorhabdotus marssoni (Bonnema, 1941)

Pl. 25, figs 24.

1941 *Cythereis marssoni* Bonnema, p.132, pl. 4, figs 67-71.

1958 *Cythereis marssoni* Bonnema. Howe & Laurencich, p. 214.

1964 *Cythereis marssoni marssoni* Bonnema. Pokorny, p. 256, pl. 2, fig. 1.

?1965 *Phacorhabdotus marssoni* (Bonnema). Damotte, pl. 6, figs 29-32.

1966 *Phacorhabdotus marssoni* (Bonnema). Deroo, p. 163, pl. 25, figs 795-797.

1968 *Pseudophacorhabdotus* sp. ex gr. *P. marssoni* (Bonnema). King, MS, p. 239, pl. 26, fig. 7.

1971 *Phacorhabdotus marssoni* (Bonnema). Damotte, pl. 5, fig. 3.

Diagnosis. A medium species of *Phacorhabdotus*, characterized by the reticulate ornament covering the entire lateral surface of each valve.

Dimensions.	L	H
RV (MPK 11636)	0.65	0.35

Depository. MPK 11635-11636

Material. 2 specimens

Remarks. This species is extremely rare in published records; its occurrence in the present study represents the first record in over thirty years, but it is possible that the synonymy is incomplete.

Damotte (1965, p. 320, present author's translation) states that "the species we call *Phacorhabdotus marssoni* is probably a sub-species of the *P. marssoni* type. It differs principally from Bonnema's original form in the ornament of the anterior part of the valve, which shows two parallel ribs separated by a polygonal network." Damotte's form is included in synonymy because the current author has not seen the original specimens on which the description is based. It is clear, however, that *P. marssoni* still needs revision, since many different subspecies exist within the *marssoni* type. If such a revision is carried out, only those specimens which conform to Bonnema's type material should be retained. King, 1968, MS, erects a new genus *Pseudophacorhabdotus* with *P. marssoni* as the type species, but the illustrated specimens are identical to the present material and the species is retained within *Phacorhabdotus*.

Donze *et al.*, 1970, in describing the assemblages from the French Senonian, illustrate three sub-forms of *Phacorhabdotus* aff. *marssoni*. These are not included in synonymy, since they are not of the same species. Form A (pl. 12, fig. 17-20) is characterized by a reticulate ornament that covers the entire lateral surface, with a predominance of longitudinal costae. This form is restricted to the Upper Coniacian and the authors note its similarity with Pokorny's subform *longisculpta*. Form B (pl. 12, figs 20-22) is intermediate between forms A and C, with a reduced ornament. Form C (pl. 12, figs 23-24) appears in the Lower Santonian and is characterized by its smooth anterior, with reticulate ornament only on the posterior section of the valve. This form is included in synonymy with *P. marssoni anteglabra* in the present study. This sub-form is more abundant, occurring in the Upper Campanian and Lower Maastrichtian at various outcrop localities.

Published range. Bonnema first reported the species from the northeastern Netherlands; Damotte (1965, 1971a) records it from the Upper Campanian of the Paris Basin, noting that it is also present in the Upper Maastrichtian of Belgium. Pokorny carried out an important revision of the species as it occurs in the Upper Cretaceous of Czechoslovakia. King's 1968 (MS) specimens were restricted to the lower *pilula* Zone (Lower Campanian) to the Upper *mucronata* Zone (Upper Campanian).

Range in this study. This species is extremely rare; occurring in the Coniacian high *coranguinum* Zone at Litcham and in the Upper Campanian Beeston Chalk at Caistor St Edmunds. In the outcrop assemblages, the species is present in the Coniacian *coranguinum* Zone, Upper Campanian basal *mucronata* and Beeston chalks.

Phacorhabdotus marssoni anteglabrus (Pokorny 1964)

Pl. 25, figs 21-23.

1964 *Cythereis marssoni anteglabra*. Pokorny, pl. 2, fig. 1.

1970 *Cythereis* aff. *marssoni* form C Donze *et al.*, pl. 12, figs 23, 24.

1998 *Imhotepia marssoni anteglabra* (Pokorny). Slipper, pl. 1, fig. K.

Diagnosis. A medium subspecies of *P. marssoni*, characterized by the complete loss of reticulation on the anterior half of the lateral valve surface

Dimensions.	L	H
LV (MPK 11634)	0. 65	0. 33

Depository. MPK 11634, specimen photographed but does not appear on plate; this species represented only by a contact print.

Material. 7 specimens

Remarks. Pokorny (1964c) working on the Upper Cretaceous of Czechoslovakia, traced the phylogenetic lines of *Cythereis marssoni* and illustrates this sub-species from the Upper Coniacian, which is identical to that of the present study from the Upper Campanian and Lower Maastrichtian, and also to that figured by Donze *et al.*, 1970, from the French Santonian. The relationship between the genus *Phacorhabdotus* and *Imhotepia* has already been discussed; Slipper's 1998 reference to *I. marssoni anteglabra* (Pokorny) has, with reference to the illustrated specimen from the Turonian of Southern England, been included in synonymy. It is identical to the material of the present study, differing only in age.

Published range. The species has previously been recorded from the Upper Coniacian of Czechoslovakia (Pokorny, 1964c) and from the Lower Santonian of France (Donze *et al.*, 1970).

Range in this study. This species ranges from Upper Campanian to Lower Maastrichtian in the outcrop assemblages; it occurs in 4 of the eighteen zones (zones 10, 11, 13, 17; basal *mucronata*, Eaton and Beeston chalks and Lower Maastrichtian pre-*Porosphaera* Beds.

Phacorhabdotus semiplicatus (Reuss, 1846)

Pl. 25, figs 13, 15, 17.

1846 *Cytherina semiplicata* Reuss, p. 104, pl. 24, figs 16a, b.

1874 *Cythere semiplicata* Reuss, p. 145, pl. 27, figs 1a-b.

1940 *Cythereis semiplicata* (Reuss). Bonnema, p. 132, pl. 4, figs 42-47.

1958 *Cythereis semiplicata* (Reuss). Howe & Laurencich, p. 233

1963 *Cythereis semiplicata* (Reuss). Pokorny, text figs 1, 3, 6-14; pl. 1, fig. 1, 2, 6.

1965 *Cythereis semiplicata* (Reuss). Szczechura, pp 519-520, pl. 2, figs 2, 3; pl. 17, figs 12, 13.

1968 *Phacorhabdotus semiplicata* (Reuss). King, MS, pp 248-250, pl. 27, figs 3-5.

non 1927 *Cythere semiplicata* (Reuss). Alexander, p. 80, pl. 6, figs 9-15.

non 1946 *Cythereis semiplicata* (Reuss). Bold, p. 90, pl. 10, fig. 12.

non 1956 *Cythereis semiplicata* (Reuss). Deroo, pl. 4, figs 65-67.

Diagnosis. A small species of *Phacorhabdotus* distinguished from another very similar species only on the grounds of its size and certain other characteristics. Two short oblique dorsal ribs, an anterior marginal rib and a short median rib across the posterior of the valve from the hemispherical sub-central tubercle. Anterior margin broadly rounded; dorsal and ventral margins nearly straight, converging towards the sub-acute posterior. Eye tubercle small but distinct.

Dimensions.	L	H
RV (MPK 11626)	0.51	0.33
LV (MPK 11627)	0.46	0.31
C (MPK 11628)	0.48	0.29
(SAG 109)	0.47	0.29

(SAG 77) 0.46 0.28

Depository. MPK 11626, 11627, 11628; assemblage slides SAG 109, SAG 77

Material. 6 specimens

Remarks. This species can be distinguished from the very similar *P. lonsdaleianus* by its smaller size and less distinct eye tubercle. Kaye, 1964a (p. 64) notes that "the multiple nature of the dorsal rib was the most diagnostic feature according to Bonnema who used this criterion for separating the form from *Cythereis semiplicata* (Reuss)." This species ranges from 0.45-0. 51 mm in its published length (see Pokorny, 1963c, text figures 1, 3, 6-14; pl. 1, figs 1, 2, 6); *P. lonsdaleianus* ranges in the present study from 0. 63 - 0. 67mm in length (Herrig's material was 0. 58-0. 65mm). The similarities between the two species, however, cannot be ignored and it is possible that they are related.

The former ranges from 0. 45 - 0. 51 mm in its published length (see Pokorny, 1963c, text figures 1, 3, 6-14; pl. 1, figs 1, 2, 6); the latter ranges in the present study from 0. 63 - 0. 67mm in length (Herrig's material was 0. 58 - 0. 65mm). The similarities between the two species, however, cannot be ignored and it is possible that they are related. In the present material, the length of measured specimens is less variable than that quoted by Pokorny and it is possible that these specimens represent late stage juveniles. King, 1968, MS, illustrates specimens which, although identical, are rather larger (0.54 - 0.57 mm in length). Specimens illustrated by Alexander (1927), Bold (1946) and Deroo (1956) are here not considered to be conspecific; they may belong to another closely related species.

In Szczechura's specimens, the ribs are slightly longer than in either those of King (MS) or the present material; they are more similar to Pokorny's illustrated specimens. This is clearly a long-ranging species which encompasses some degree of morphological variation.

Damotte, 1964, p. 106, illustrates a new species from the Lower Campanian of France; *Phacorhabdotus strangulans* (pl. 1, fig. 7a-d, pl. 2, fig. 11a-b) is similar to the present material, but the latter species has a more depressed anterior, the females are less elongate and broader, the anterior margins more broadly rounded and the carapace is different in dorsal view. The lateral surface in *P. strangulans* is also smoother and the valve appears slightly more heavily calcified.

Published range. Pokorny, 1963, illustrates species from the Coniacian of Bohemia. Szczechura, 1965, records it from the Campanian to Palaeocene of Poland. King, 1968, MS, gives a range of Upper Campanian *mucronata* Zone to Lower Maastrichtian *lanceolata* Zone for this species in Norfolk and Northern Ireland, noting that "in Norfolk this species is rare above the lowest Beeston Chalk" (p. 250).

Range in this study. The species occurs as a rare component in the Beeston Chalk of the Trunch Borehole. It also occurs in the basal *mucronata* Chalk at Cringleford and in the lowest sample of the Paramoudra Chalk at Crown Point Pit, Whitlingham. It is restricted to the Upper Campanian in the Trunch Borehole and the outcrop localities. It is restricted to 3 zones out of the 18 studied (10, 13, 14; basal *mucronata*, Beeston and Paramoudra chalks), but this is perhaps an artefact of the paucity of specimens rather than a true stratigraphical range.

Family XESTOLEBERIDIDAE Sars, 1928
Genus XESTOLEBERIS Sars, 1866.

Treatise reference. Q343.

Treatise diagnosis."Carapace ovate, LV larger than RV. Hinge merodont with elongate crenulate terminal cusps in RV, separated by somewhat curved to nearly straight, finely crenulate to smooth furrow; marginal area narrow, except in front where vestibule is present; radial canals short, straight, adductor scars in vertical row of 4, with arrow-head shaped antennal scar in front and 2 mandibular scars in front; crescent shaped scar above this group in eye region. *Cret.-Rec.*

Remarks. The above diagnosis is adequate but needs revision to incorporate the wider morphological range shown by species erected since the genus was first described. Weaver (1982) included a size range and details about the nature of the dorsal margin but this is not arched in all species. The following diagnosis is that of Weaver; followed by a further emendation by the present author.

Diagnosis. (Weaver, 1982, p. 96); " Size small to medium, carapace egg shaped with strongly convex dorsal margin. Surface smooth. Hinge of right valve with crenulate terminal teeth separated by curved groove. marginal zone with vestibule at anterior."

Emended diagnosis. Size small to medium, carapace ovate to elongate, often with strongly arched dorsal margin; surface smooth and featureless, or with opaque patches. *Xestoleberis* spot variable, not always present. LV larger than RV. Hinge antimerodont with elongate dentate terminal bars in RV, separated by a slightly curved or straight, locellate furrow; marginal zone narrow, except in anterior where vestibule is present; radial canals short, straight, adductor scars in vertical row of 4, with sagittate antennal scar in front and 2 mandibular scars antero-ventrally; crescent shaped scar above this group in eye region.

Palaeoecology. Most species of this genus are phytal in habit, living on angiosperms and algae in the photic zone. Other species living on or interstitially within the sediment itself are lower and more ventrally flattened (pers. comm. Whatley, June 2000). High abundance is generally indicative of near shore environments, although some species are recorded from the deep sea (e.g. Benson, 1961; Whatley & Coles, 1987). Intermediate between deep water and those species adapted for life in tidal pools, are the normal marine species of the shelf. These are represented by many species in the late Mesozoic and may be strongly influenced by the nature of the bottom sediment.

In the present study, and in the Lower Chalk and Cenomanian Plenus Marls of Southern England (Weaver, 1982, p. 96), the genus is a rare component. Its rarity in both studies supports the assumption that the majority of Cretaceous species were not phytal (and therefore not near-shore). Weaver's species, *X. burnetti, X. planus,* are both rather flattened, the former being "slightly more common in the Lower Cenomanian," the latter rare throughout. The material of the present study comprises 4 species, of which *Xestoleberis ovata* Bonnema is by far the most common; it is similar in shape to phytal representatives of the genus, but is much smaller. Another species, X. cf. *X. planus,* is lower and its carapace is more elongate, less inflated and ventrally flattened. In the Trunch Borehole, the genus is represented by two of the four species and is restricted to the Campanian, with relatively short stratigraphical ranges and clear origination and extinction levels. In the assemblages of the

various outcrop localities, the genus occurs throughout the Norfolk Basin and has a more extensive range. All species occur in the Coniacian and one species (*Xestoleberis* sp. 1) is restricted to this interval. The genus is absent in the Santonian and Lower Campanian, possibly becoming locally extinct due to lowered oxygen levels in the area at this time, and is most common in the Upper Campanian and Lower Maastrichtian. The longer range could be the result of a number of factors, such as localised substrate or depth variations, but it would be extremely difficult to assess the exact nature of these contributory factors. The genus itself, from the published records of Cretaceous species, is an extremely variable one in terms of size, shape and degree of valve tumidity. It is interesting to note that, in a detailed analysis of ostracods from the late Jurassic to early Cretaceous of Eastern England, Wilkinson (1988, MS) did not encounter any species of the genus. The published range is Cretaceous to Recent, but Weaver notes its occurrence in the Lower Chalk and Cenomanian Plenus Marls. It is reasonable to assume that, although the genus first appears in the Lower Chalk and Cenomanian in Southern England, it does not occur until the Coniacian in East Anglia and is a Lazarus genus throughout the Santonian and Lower Campanian.

Xestoleberis ovata Bonnema, 1940

Pl. 26, figs 9-13, 15.

1940 *Xestoleberis ovata* Bonnema, p. 43, pl. 7, figs 39-45.

1958 *Xestoleberis ovata* Bonnema. Howe & Laurencich, p. 517.

1965 *Pulaviella ovata* (Bonnema). Szczechura, pp 553-554, pl. 1, figs 7-8; pl. 8, figs 25-27.

1968 *Pulaviella ovata* (Bonnema). King, MS, pl. 38, figs 11, 12.

1974 *Xestoleberis ovata* Bonnema. Gründel, pl. 2, figs 9-11.

1998 *Xestoleberis ovata* Bonnema. Slipper, pl. 1, fig. P.

Diagnosis. A medium species of *Xestoleberis* characterised by its rather inflated carapace, arched dorsal margin and rounded posterior, anterior and ventral margins; a clear *Xestoleberis* spot in most individuals; surface smooth and moderately calcified; few opaque patches.

Dimensions.	L	H
LV (MPK 11833)	0.45	0.29
LV (MPK 11834)	0.44	0.26
RV (MPK 11803)	0.44	0.26
LV (MPK 11804)	0.45	0.29
RV (MPK 11805)	0.38	0.21
LV (MPK 11806)	0.40	0.24

Depository. MPK 11801, 11802, 11803, 11804, 11805, 11806.

Material. At least 50 specimens.

Remarks. This is the most abundant representative of the genus, belonging to a shallow marine group of species rather than a phytal or neritic species group. It is clearly distinguishable from the other species

in this study, by its shape (ventral margin rounded; in X. cf. *X. planus* Weaver (1982) this feature is straight and flattened). It is also more inflated than Weaver's species or the material of the present study (cf. *X. planus),* and less elongate. It is smaller than *Xestoleberis* sp. 1 & 2 and exhibits a clear *Xestoleberis* spot in most individuals. Slipper (1998) illustrates a specimen from the Turonian/Coniacian of Dover with a less rounded dorsal margin than that of the present study and Bonnema's original material from the Maastrichtian of the Netherlands. It is included in synonymy but may represent an earlier closely related species. *X. marssoni* Bonnema (1940, p. 43, pl. 7, figs 46-50), also illustrated by Slipper (pl. 1, fig. O) is extremely similar to *X. ovata* as illustrated by other authors, but has a slightly greater breadth and a more narrowly rounded anterior margin. *Xestoleberis cf. X. tunisiensis* Esker (Viviere, 1985, pl. 27, figs 13-14) from the Santonian of Northeastern Algeria is similar in the shape of its dorsal, anterior and posterior margins. The ventral margin is less rounded, however, and the carapace is much less inflated in ventral or dorsal view. *X. obesa* Van den Bold (1964, pl. 14, fig 10a-b), from the Cenomanian and Turonian of Egypt, is similar in size and shape but the carapace is more inflated than *X. ovata.*

King, 1968, MS, (p. 354) referred this species to the subgenus *Pulaviella* dividing *Xestoleberis* into *Xestoleberis (Xestoleberis)* Sars, 1866, and *Xestoleberis (Pulaviella)* Szczechura, 1965, based on hinge differences. He states that "the generic separation of these two types is unjustified and *Pulaviella* is, therefore, included as a subgenus of *Xestoleberis.*" The present author rejects this and believes that *Pulaviella* which allegedly differs from *Xestoleberis* in its "simple hinge", is merely *Xestoleberis* with a more weakly expressed antimerodont hingement. In plate 26, figs 9-13, 15, some amelioration can be seen on the median element of LV and some loculation especially posteriorly in the terminal elements.

Published range and distribution. Originally described by Bonnema from the Schreibkreide and Mergel of Holland. It has also been reported from the Turonian/Coniacian of Dover (Slipper, 1998) and the Santonian of Austria (Gründel, 1974). King, 1968, (MS, p. 358) notes that "the species has been found throughout the Campanian of Norfolk, the Isle of Wight and Northern Ireland and in the lowermost Maastrichtian of Norfolk and Northern Ireland."

Range in this study. In the Trunch Borehole, the species ranges from the middle of the Lower Campanian *Gonioteuthis quadrata* Zone (zone/subdivision 9; First Appearance Datum FAD = SAG 504) up to the upper part of the Upper Campanian Weybourne Chalk (zone/subdivision 12; Last Appearance Datum LAD = SAG 363); it reaches a maximum abundance of six specimens (6% of assemblage) in SAG 408 (basal Weybourne Chalk). In the outcrop assemblages, the species is present in 5 out of the 18 zones. It first appears in the Upper Campanian basal *mucronata,* Eaton, Beeston and Paramoudra chalks (zone/subdivisions 10-11, 13-14) to the Lower Maastrichtian pre-*Porosphaera* Beds (15)

Table 2.9 (p. 271) compares and contrasts the diagnostic characteristics of *Xestoleberis* and *Uroleberis.* It was compiled by the present author from the original diagnoses of *Xestoleberis* Sars, 1866 and *Uroleberis* Triebel, 1958.

Table 2.9. *Uroleberis* and *Xestoleberis* - diagnostic characteristics of the two genera

	Xestoleberis Sars, 1866	*Uroleberis Triebel, 1958*
ornament	surface smooth and shiny; in some some cases opaque spots occur	Surface smooth or pitted; valves heavily calcified
shape	egg-shaped; dorsal margin convex; ventral margin sinuous. Posterior end end more broadly rounded; no caudal caudal process; anterior end evenly to acutely rounded in lower half	carapace short and high with convex dorsal margin; posterior end with clear caudal process; anterior end obliquely rounded below; valves strongly inflated
size range	0. 40 - 0. 70 mm in length	0. 50 to 0. 75 mm in length
inner lamella	wide throughout; marginal zone narrow at anterior where line of concrescence and inner margin are widely separated; elsewehere, they coincide and run sub-parallel to outer margin	rather narrow at anterior; inner margin and line of concrescence is separated anteriorly; in ventral and posterior regions they coincide
marginal pore canals	anteriorly 12-20 straight short simple marginal pore canals	about 30 in type species; all straight and simple
hinge structure	antimerodont; terminal teeth in RV crenulate; crenulation continues over short distance on both ends of median hinge element which consists of a strongly curved ridge in LV and a groove in RV; no accomodation groove	antimerodont; terminal teeth in RV crenulate, connected by a narrow smooth ridge; between ridge and dorsal margin runs a groove. LV corresponding crenulate sockets, narrow accommodation groove
schematic of hinge (Van Morkhoven , 1963, figs 746 and 755 type species:	 LV *Xestoleberis depressa*	 LV *Uroleberis parnensis*
ecology	littoral to epi-neritic	epi-neritic
muscle scars	generally consist of 4 adductor muscle scars and a V-shaped, kidney or heart-shaped frontal scar	4 widely spaced adductors and a V-shaped frontal scar
eye spots	external eye spots absent, internal *Xestoleberis* spot may be present	external eye spots absent, internal *Xestoleberis* spot may be present

Xestoleberis cf. *X. planus* Weaver, 1982.

Pl. 26, figs 20, 21.

cf 1982 *Xestoleberis planus* Weaver, pl. 19, figs 9-11

Diagnosis. A medium, elongate species of *Xestoleberis* with a ridge along the junction between flat ventral surface and inflated lateral surface of each valve. Surface smooth with no opaque patches; *Xestoleberis* spot not evident.

Dimensions.	L	H
(MPK 11812)	0.56	0.36
(MPK 11813)	0.57	0.37

Depository. MPK 11812, 11813.

Material. 15 specimens.

Remarks. *Xestoleberis* cf. *X. impressa* (Reuss, 1851), figured by Colin, 1974 (pl. 6, fig. 15) from the French Upper Cenomanian to Lower Turonian, is rather similar to both Weaver's species and the present material. It is smaller and slightly more elongate. The present material differs from the type material in that it lacks the distinctive hinge used by Weaver to distinguish it from other Cretaceous species (p. 97) "hinge of right valve consists of a low crenulate posterior tooth with gently curved smooth groove in front. This species has the characteristics of *Xestoleberis,* except that its hinge is more similar to that in *Uroleberis* Triebel, 1958, in that it has a groove above the hinge bar in the left valve and the hinge bar is not crenulate, but has very poorly developed terminal teeth in the right valve". Table 2.9 contrasts the diagnostic characteristics of *Xestoleberis* and *Uroleberis.* The absence of a caudal process suggests that it does not belong in *Uroleberis.* The present material is almost identical in shape, with the same flat ventral surface, but is slightly less elongate and has fewer ridges on the ventral surface. It is, therefore, only compared to Weaver's species.

Published range and distribution. Weaver first described the species from the Middle Cenomanian of Pitstone, Hertfordshire, and Bluebell Hill, Kent.

Range in this study. In the Trunch Borehole, it first appears in the Lower Campanian *G. quadrata* Zone (FAD= SAG 484) and ranges into the Upper Campanian basal *mucronata* Chalk (10; LAD= SAG 414). In the outcrop assemblages, the range is more extensive, but a little sporadic. It occurs in 4 zones (3, 10-11, 14; Coniacian *Coranguinum* Zone, Upper Campanian basal *mucronata*, Eaton and Paramoudra chalks).

Xestoleberis sp. 1

Pl. 26, figs 14, 16.

Diagnosis. A medium, moderately inflated species of *Xestoleberis;* anterior margin broadly rounded, posterior margin slightly oblique, dorsal margin arched, ventral margin slightly concave. Lateral surface smooth with large, circular pores.

Dimensions.	L	H
(MPK 11807)	0.54	0.38

(MPK 11808) 0.54 0.35

Depository. MPK 11807, 11808

Material. 2 specimens.

Remarks. Left in open nomenclature because of its sparse record, but probably new, this species can be distinguished from *X. ovata* and *X. cf. X. planus* by its size and shape and by the number of large, round pores on its lateral surface. No *Xestoleberis* spot evident, but this may be obscured by adherent matrix. Hinge not seen or poorly preserved but clearly, this species belongs to *Xestoleberis* due to its shape, smooth lateral surface, and certain other details of morphology. It cannot be assigned to *Uroleberis* due to the lack of any caudal process. The species is similar to specimens tentatively assigned to *Xestoleberis (Pulaviella) marssoni* (Bonnema, 1941) by King, 1968 (MS, pl. 38, figs 9-10), but is probably not conspecific.

Range in this study. Absent in the Trunch Borehole and restricted to the Coniacian *coranguinum* Zone (3) and Upper Campanian Paramoudra Chalk (14) in the outcrop assemblages.

Xestoleberis sp. 2.

Pl. 26, figs 17-19.

Diagnosis. A small to medium, rather elongate species of *Xestoleberis;* dorsal margin weakly arched; anterior and posterior margins rounded, ventral margin straight

Dimensions.	L	H
(MPK 11809)	0.48	0.30
(MPK 11810)	0.46	0.32
(MPK 11811)	0.45	0.32

Depository. MPK 11809, 11810, 11811

Material. 3 specimens.

Remarks. Left in open nomenclature due to its rarity, This species can be distinguished from *X. ovata* and *X.* cf. *X. planus* by its size and shape. It is, however, closer to the former. It could not be assigned, or even compared, to any other Cretaceous representative of this variable and problematical genus.

Range in this study. This species was not found in the assemblages of the Trunch Borehole; it is a rare species and is restricted to the Upper Campanian.

Superfamily : CYTHERACEA

Family: UNCERTAIN

Genus: NEOCYTHERE Mertens, 1956.

The classification used in the 1961 *Treatise* and by most post-*Treatise* workers (Van Morkhoven, 1962, 1963; Kaye, 1963, 1964; Benson & Tatro, 1964; Hartmann, 1964; Herrig, 1965, 1966; Grundel, 1968; King, 1968, MS; Damotte, 1971a; Babinot, 1980, Weaver, 1982; Robaszynski et al., 1985; Bless, 1988; Bless et al., 1988; Witte et al., 1992; Symmonds, 1996, MS, and others) is that this genus belongs in the Progonocytheridae Sylvester-Bradley, 1948, Progonocytherinae Sylvester-Bradley, 1948,

Family PROGONOCYTHERIDAE Sylvester-Bradley, 1948

Subfamily PROGONOCYTHERINAE Sylvester-Bradley, 1948

Genus NEOCYTHERE Mertens, 1956

Treatise diagnosis. Shape ovate to sub-ovate, with broadly rounded anterior margin and straight dorsal margin. Valves strongly inflated. Hinge merodont to amphidont; median bar in left valve usually crenulate, terminal teeth in RV usually strongly crenulate, sometimes with an antero-median tooth.

Remarks. The genus *Neocythere* was erected by Mertens for forms similar to *Cythere concentrica* Reuss, but with an amphidont hinge and an accommodation groove in the left valve. Kaye, 1963, in a study of the genus in the Speeton Clay (p. 274) notes that there is "a great deal of uncertainty about the interpretation of the forms related to this group and, until quite recently, all Cretaceous Ostracoda having concentric ornament, and slight ventral tumidity were referred to *Cythere concentrica* Reuss."

Mertens, 1956, worked extensively on these forms and redescribed Reuss' type material. Problems with preservation, most importantly in the preservation of the hinge, did not allow for correct generic assignment and the species was left tentatively within the genus "*Cythere*". *Neocythere* was distinguished on the basis of hinge structure. Kaye, on examination of the hinge structure in species referred to the genus "*Cythere*" found (1963, p. 275) that they differ from *Neocythere* in being symmetrically merodont and having no accommodation groove in the left valve. These differences are, in Kaye's opinion, "insufficient to warrant generic separation". In Kaye's work on the Speeton Clay of East Yorkshire, *Neocythere (sensu stricto)* was used for forms with an amphidont hinge, while a new subgenus *Physocythere* was erected to accommodate the forms grouped by Mertens under "*Cythere*", with a merodont hinge.

Neocythere (Neocythere): type species = *Neocythere vanveeni* Mertens, 1956; (see Kaye, 1963, p. 276 , pl. 41, fig. 23, 25): generic diagnosis according to Kaye: "a subgenus of *Neocythere* (s.l); including forms similar to the genotype having an inflated, ventrally tumid carapace. The hinge in the right valve consists of two terminal crenulate teeth, between which is a locellate furrow deepened at its anterior end to form a smooth circular socket. The left valve is complementary and possesses a distinct accommodation groove above the median element.

Neocythere (Physocythere): type species = "*Cythere*" *lingenensis* Mertens, 1956 (see Kaye, 1963, pp 277-278, pl. 41, figs 15-22, 24): generic diagnosis according to Kaye: "a sub-genus of *Neocythere* (s.l), showing the characteristic inflated ventrally tumid shape of the genus but differing from *Neocythere sensu stricto* in the structure of the hinge. The hinge is symmetrical, consisting in the right valve of two strong terminal, crenulate cusps separated by a long, straight, locellate groove. In the left valve, there is no accommodation groove, but a wide shelf occurs above the median element, sloping down to the dorsal margin. The hinge elements, as a whole, are much stronger than in *Neocythere*."

The material of the present study, especially *Neocythere virginea* (Jones,1849) is characterised by its inflated, tumid carapace and antimerodont, strongly developed hinge structure. *N. virginea* sometimes appears in synonymy as *Neocythere (Physocythere) virginea* (e.g. Kaye, 1966; Herrig, 1966; Neale, 1978,

Bless, 1988). If plate 41 of Kaye, 1963, is examined closely, the hinge structure of the specimens from the present study appears very like those in species assigned to the subgenus *Physocythere*, but the present author agrees with Weaver, 1982, in considering this genus to be simply a synonym of *Neocythere*.

Mertens, 1956, also erected the genus *Centrocythere* to include species with similar shape and ornament, but with a strongly amphidont-type hinge, a high, step like anterior tooth in the RV and a strong anteromedian tooth in the left. Kaye, 1963 (p. 275), regards these differences to be of sub-generic status (also Van Morkhoven, 1963, p. 214, 260). The present author is in agreement with these latter authors.

Neocythere (Centrocythere): subgenotype: *Centrocythere denticulata* (Kaye, 1963, pl. 41, fig. 13). The diagnosis according to Kaye is as follows: "a subgenus of *Neocythere sensu lato* showing the usual inflated shape and ventral tumidity, but having a characteristic hinge arrangement. In the right valve, the anterior tooth is step-like; the back portion being twice as high as the front. The posterior tooth is crenulate, and the median element consists of a locellate furrow, deepened at its anterior end to form a smooth socket. There is an accommodation groove above the median element in the left valve."

Neocythere is a problematical genus in need of revision. Weaver, 1982, discusses the problem of taxonomy in some detail. The type species of the genus is *Neocythere vanveeni* Mertens, from the Albian of Germany. In typical Albian specimens, the hinge in the right valve has broad, flat, crenulate teeth, separated by a denticulate median groove. This is deepened slightly at its anterior end to accommodate a small antero-median tooth. Specimens of *N. vanveeni* from the uppermost Albian show a progressive loss of this tooth and specimens from the Cenomanian have no antero-median tooth at all. The presence of an antero-median tooth is, therefore, not a stable characteristic and should not be used as a diagnostic feature. In any case, the type hinge should not be described as "amphidont" - which hinge type (*sensu stricto)* is confined to the ornate Trachyleberididae, Hemicytheridae and Thaerocytheridae.

Whatley and Ballent, 1996, in reviewing the genus *Progonocythere* and its close allies, redefine the Progonocytheridae. In the *Treatise* revision, the Progonocytheridae will contain only those taxa with entomodont or lobodont hinges (p. 920). The family will be divided into the Progonocytherinae, comprising sub-ovate to sub-triangular genera with a convex dorsal margin and a more or less strong ventro-lateral tumidity, and a second sub-family which will include sub-rectangular to sub-quadrate forms. *Neocythere*, based on external characteristics, would be placed within the Progonocytherinae. It is a strongly inflated, sub-ovate form with a convex dorsal margin but, when the internal hinge morphology is examined, it becomes clear that the genus does not belong in either Progonocytheridae or Progonocytherinae. The hinge is amphidont to merodont. In the case of the most common representative of the genus in the present study, *Neocythere virginea* (Jones, 1849) has a merodont/antimerodont hinge consisting, in the right valve, of terminal dentate bars separated by a locellate groove. In the LV, there are two loculate sockets separated by a strong denticulate bar. Above the median element, there is a broad but shallow depressed shelf. This is evident in the illustrated specimens (plate 27 of this thesis, figs 1-19).

Symmonds, 1996 (MS., p. 32), discusses the familial position of *Neocythere* and notes that, although four out of the five species present in the Lower Cenomanian of Morocco (assigned to both

Physocythere and *Centrocythere*) show no entomodont hinge, one species does show such a hinge type. There is, therefore, "some justification for retaining the position of the genus within the Progonocytheridae." There is, however, more evidence against it belonging in this niche, since the majority of forms do not have the diagnostic entomodont hinge structure used by Whatley and Ballent to redefine the family. Whatley (verb. comm., November 2000) does not consider the material described by Symmonds (which he has seen) as being possessed of true entomodont hingement. He would describe it as antimerodont.

Wilkinson, 1988a, MS, concludes that *Neocythere* should, therefore, be classed as either an indeterminable genus (Gen. indet) or a new family or sub-family erected to accommodate it (i.e. Neocytheridae or Neocytherinae). This work is unpublished and follows what will be in the revised Treatise. Wilkinson (1988, p. 321) includes *Neocythere* and the subgenera *Physocythere* and *Centrocythere* in a new family: Neocytheridae, as well as other genera such as *Pneumatocythere* Bate, *Micropneumatocythere* Bate and *Merocythere* Oertli. However, the present author notes that the last three constitute a distinct group within the Cytherideidae. One of the main difficulties in dealing with Neocytherids is their lack of either obvious ancestors or descendants. They differ too much from Progonocytherids to seek ancestry there and contemporary cytherideinids show no morphological similarities. The probability is that they have arisen by a quantum morphological change, as a process of punctuated equilibrium but the question of which cytheracean group from which they arose remains obscure. The groups themselves, while all very similar in their globular carapace morphology and, to a certain degree, in ornamentation, demonstrate a potential for divergence as witnessed by differences in the nature of hingement between the various subgenera.

Without further work, the erection of a new family is not really justifiable. Until more is known about the origins of this problematic group, it is probably better to leave it in family *incertae sedis*.

Neocythere sp. cf. *N. inornata* Colin, 1974

Pl. 27, fig 12.

cf 1974 *Neocythere (Physocythere) inornata* Colin, pp 36-37, pl. 10, figs 7-10.

Diagnosis. A rather elongate, medium species of *Neocythere*, with only faint concentric striations. Dorsal and ventral margins straight, anterior and posterior margins narrowly convex.

Dimensions.	L	H
MPK 11824	0.53	0.32

Depository. MPK 11824

Material. Fewer than 10 specimens.

Remarks. Colin gives a size range of 0.54-0.71 mm in length; the present material falls into the lowest part of this range. It is possible that these specimens are juveniles but this cannot be proven. The etymology of this species reflects the almost total absence of concentric striations seen in such species as *Neocythere virginea* and other Cretaceous forms. The present material is very similar to that figured by Colin, 1974, and Babinot *et al.*, 1985, but is smaller and slightly less elongate and a little more ornate.

Published range. Colin first described this species from the Upper Cenomanian of Southern France and Portugal. Babinot *et al.*, 1985, report it from the Cenomanian of Aquitaine.

Range in this study. This species is restricted in its stratigraphical range, occurring in only three of the eighteen zones studied; the Lower Campanian restricted *Gonioteuthis quadrata* Zone (9) and in the Upper Campanian basal *mucronata* Chalk (10) and Eaton Chalks of certain outcrop localities.

Neocythere virginea (Jones, 1849)

Pl. 27, figs 1-11, 13-19.

1849 *Cythere punctatula virginea* Jones, p. 12, pl. 1, fig. 2.

1890 *Cythere concentrica* var. *virginea* Jones. Jones & Hinde, p. 32, pl. 1, figs 14-17.

1938 *Cythere slavantensis* Van Veen, pl. 1, figs 9-15.

1940 *Cythere slavantensis* Van Veen. Bonnema, p. 129, pl. 4, figs 1-4.

1964 *Neocythere (Physocythere) virginea* (Jones). Kaye, p. 48, pl. 1, figs 11, 14-17.

1965 *Neocythere (Physocythere) virginea* (Jones). Szczechura, p. 548, pl. 4, figs 8-9; pl. IX, figs 5-8.

1965 *Sphaeroleberis saccata* (Marsson). Damotte, pl. 4, figs 37, 39.

1966 *Neocythere (Physocythere) virginea* (Jones). Herrig p. 857, pl. 25, figs 3-9; pl. 27, figs 1-3; text figs 93, 95, 96.

1966 *Sphaeroleberis saccata* (Marsson). Deroo, p. 125, pl. 12, figs 449-454.

1968 *Neocythere (Physocythere) virginea* (Jones). King, MS, pl. 10, figs 4, 6, 8, 9-12.

1971a *Neocythere virginea* (Jones). Damotte, p. 105, pl. 7, fig. 5.

1978 *Neocythere (Physocythere) virginea* (Jones). Neale, p. 358, pl. 13, fig. 10.

1985 *Sphaeroleberis saccata* (Marsson). Robaszynski *et al.*, pl. 9, fig. 9.

1988 *Neocythere virginea* = *Physocythere virginea* (Jones). Bless *et al.*, pl. 2, figs K - L.

?1992 *Neocythere* sp. A Weaver. Witte *et al.*, pl 4, fig. 9.

Diagnosis. A medium, ovate to subovate species of *Neocythere* which is strongly tumid; dorsal margin strongly convex. Lateral surface with variable concentric ribbing on the antero-vantral, postero-ventral and ventral surfaces of each valve. Hinge strongly developed and antimerodont.

Dimensions.	L	H
LV (MPK 11814)	0.75	0.45
LV (MPK 11815)	0.78	0.45
LV (MPK 11816)	0.80	0.45
LV (MPK 11817)	0.75	0.45
RV (MPK 11818)	0.68	0.41
LV (MPK 11819)	0.76	0.46
RV (MPK 11820)	0.67	0.35
LV (MPK 11821)	0.70	0.37
RV (MPK 11822)	0.65	0.35
LV (MPK 11823)	0.71	0.37

LV (MPK 11825)	0.71	0.37
LV (MPK 11826)	0.68	0.40
RV (MPK 11827)	0.63	0.34
RV (MPK 11828)	0.67	0.41
RV (MPK 11829)	0.70	0.41

Depository. MPK 11814-11835; species slide a and b (Trunch Borehole), c and d (outcrop localities).

Material. More than 1000 specimens.

Remarks. This is an abundant species in the present study and well documented in the Cretaceous of Britain and Europe. It is, however, variable in its size and shape and shows strong sexual dimorphism. A full ontogeny occurs in the present study, although the majority of specimens were adult, with more elongate and less inflated males and more tumid and less elongate females. A clear change in valve shape can be documented from the rather angular juveniles to the tumid adults, which also have more strongly arched dorsal and ventral margins. Juveniles sometimes also exhibit a slightly angular posterior. This is, however, less pronounced than in the individual left in open nomenclature as *Neocythere* sp. 1, which is clearly juvenile but cannot be attributed to any other species of the genus in the present study.

Kaye (1964, p. 48) in describing the hinge notes that it consists, "in the right valve, of terminal denticulate teeth separated by a locellate groove. In the left valve, there are two divided sockets separated by a strongly denticulate bar. Above the median element is a broad, shallow depressed shelf." The type species, *N. vanveeni,* from the Middle Albian of Germany, is similar to *Neocythere virginea* but the concentric ornament is less pronounced and the dorsal margin less arched. The diagnostic accommodation groove is absent in the former species.

The ornament of *Neocythere virginea* in the present study was very variable, ranging from individuals with welll developed concentric ribbing to others which are nearly smooth. Such variation often occurs in the same assemblage and has also been noted by many other workers. Specimens picked by the current author from a small sample from the Campanian Sonning Flint Meal of Berkshire (found as a residue in the University of Aberystwyth Micropalaeontology collections) can be compared with the material from East Anglia. Specimens from Sonning were very similar to the present material, but generally had a more strongly developed concentric ornament. This is almost certainly due to the better preservation (unaffected by diagenesis) of the Berkshire material.

Damotte, 1971a (p. 105), writing of a personal communication to Herrig in 1967, states that Deroo's form of *Sphaeroleberis saccata* is not conspecific with Marsson's original species. It is, however, probably synonymous with *Cythere punctatula virginea* of Jones and Hinde, 1890 = *Neocythere virginea* (Jones). When illustrated specimens are compared, the similarities are obvious and Deroo's specimens are, therefore, considered in the present synonymy to be a junior synonym of *Neocythere virginea*. Kaye, 1964, considers *Cythere slavantensis,* as figured by Van Veen, 1938, and Bonnema, 1940, to be conspecific with *Neocythere virginea.* The present author, after examination of both Veen and Bonnema's illustrations and taking into account the relatively poor quality of these, is in agreement.

Weaver, 1982 (p. 49, pl. 8, figs 4-6) figured several specimens with a very weak pattern of concentric ornament. Witte *et al.*, 1992, illustrate a specimens assigned to Weaver's species A, which is probably a juvenile of either *Neocythere virginea* or *N. vanveeni.*

Interestingly, in the present study, this species is frequently the second dominant species after *Cytherella ovata*, or less commonly *Cytherelloidea granulosa*. This is the case even during periods of kenoxia where other podocopids decline or disappear as Lazarus taxa and there is a strong correlation between *Neocythere virginea* and *Cytherelloidea granulosa.* This is discussed in more detail in Chapter 4 of this thesis with quantatitive data. This relationship has not been cited in previously published work by other authors and is not necessarily the case at all localities in the present study; it is, however, very clear in the Upper Campanian Beeston Chalk assemblages at Caistor St Edmund and in the Paramoudra Chalk at Crown Point Pit, Whitlingham.

Published range. King, 1968, MS, notes that the range in the English Chalk is *coranguinum* Zone (Coniacian) to Lower Maastrichtian. In Northern Ireland, the published range is slightly more restricted (Campanian - Lower Maastrichtian).

Range in this study. This species is abundant and well-represented in the Upper Chalk of East Anglia in both the outcrop assemblages and those of the Trunch Borehole. Its stratigraphical range is Coniacian to Lower Maastrichtian (outcrop); Santonian to Lower Maastrichtian (Trunch Borehole), but the species is most common in the Upper Campanian to Lower Maastrichtian. It is one of the few podocopid taxa to conntinue across the Santonian and Lower Campanian, when most other deposit feeders either decline or disappear. At Trunch, it first appears in the lowest Santonian samples (*Marsupites testudinarius* Zone, FAD SAG 647) and occurs in most samples upwards into the Lower Maastrichtian pre-*Porosphaera* and *Porosphaera* Beds of the *Belemnella lanceolata* Zone. In the outcrop assemblages, the species is usually ubiquitous in all samples in sixteen of the eighteen zones studied, but is absent in the Santonian *Uintacrinus socialis* Zone and the Lower Campanian *pilula* Zone. It is especially abundant in the Upper Campanian Beeston Chalk at Caistor St Edmunds.

Neocythere sp. 1

Pl. 27, fig. 20

Diagnosis. A medium species of *Neocythere;* rather inflated and with a broad anterior margin and an acute, narrow posterior margin; faint, narrow marginal rim parallel to anterior and posterior margins; dorsal margins short and straight. Ventral margin convex; lateral surface smooth with only weakly developed concentic ornament on antero-ventral area of valve.

Dimensions.	L	H
left valve (MPK 11830)	0.53	0.34
(SAG 404)	0.55	0.34
(SAG 404)	0.51	0.30

Depository. MPK 11830

Material. 4 specimens.

Remarks. Left in open nomenclature because of its rarity, this species is similar in size, shape and ornament to *Neocythere carcaveloensis* Andreu, from the Lower Albian of Portugal. It may represent late-stage juvenile individuals of a species not seen in the material of the present study in adult form, but this can not be determined due to the relatively poor state of preservation. Juveniles of *Neocythere virginea* in the present study sometimes also exhibit a slightly angular posterior. This is, however, less pronounced than in the individuals left in open nomenclature as *Neocythere* sp. 1, which are clearly juvenile but cannot be attributed to any other species of the genus.

Range in this study. This species is rare and has a restricted stratigraphical range: Lower Campanian *Gonioteuthis quadrata* Zone to the Upper Campanian Paramoudra Chalk in East Anglia. In the outcrop samples, it is present in five of the 18 zones, occurring in the Lower Campanian *Gonioteuthis quadrata* Zone (9) and the Upper Campanian Eaton, Weybourne, Beeston and Paramoudra chalks (11, 12, 13, 14). In the Trunch Borehole, it occurs in the Lower Campanian *Gonioteuthis quadrata* Zone.

Neocythere sp. 2.

Pl. 27, fig. 21

Diagnosis. A medium species of *Neocythere*, with a rounded anterior margin and an arched dorsal margin. Weak concentric striae visible.

Dimensions.	L	H
LV (MPK 11831)	0.52	0.33

Depository. MPK 11831

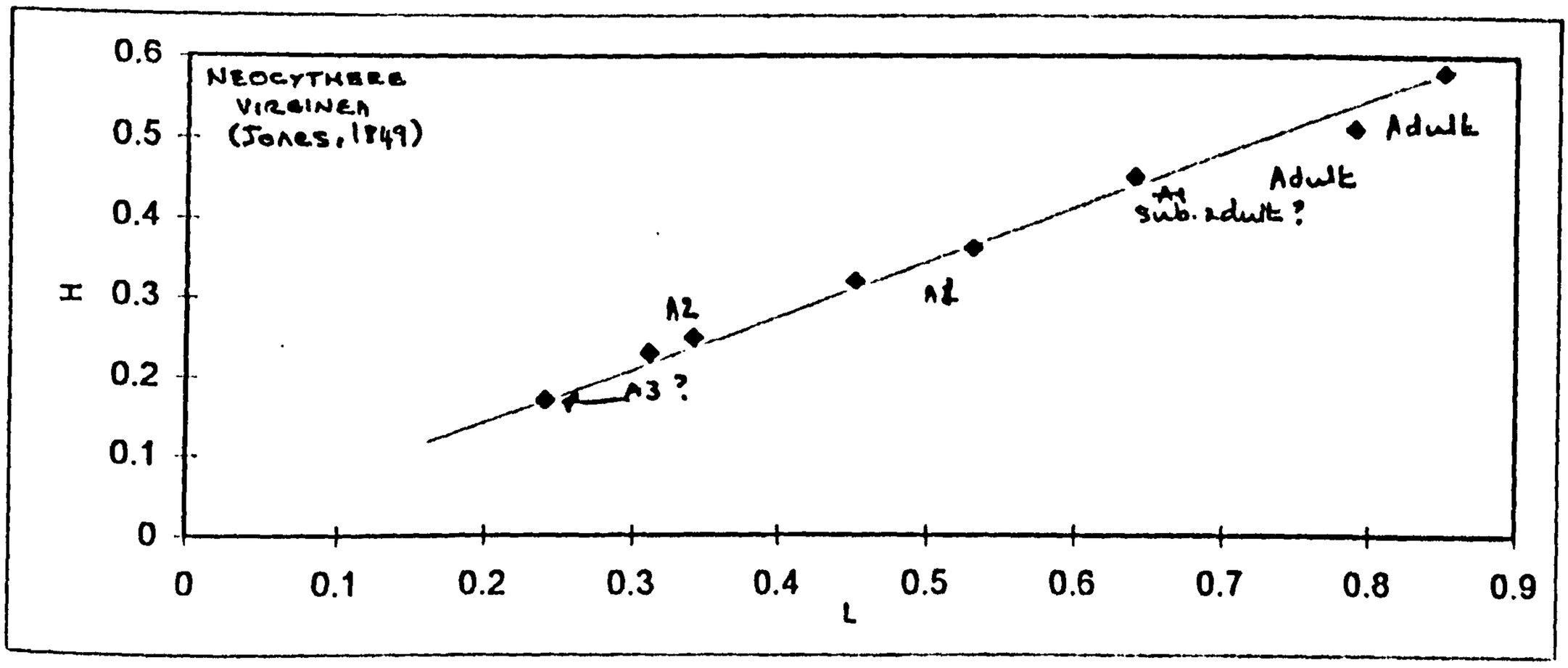
Material. A single specimen.

Remarks. Almost certainly a juvenile but not clearly attributable to any representative species of *Neocythere* seen in the present study, this species is left in open nomenclature due to its rarity.

Range in this study. Restricted to the Lower Maastrichtian *Porosphaera* Beds of Sidestrand (Zone/subdivision 16).

King (1968 MS) records over 2000 specimens of this species from the British Chalk. A full ontogeny is recorded with four, instar stages identifiable from the dimensions given in the systematic taxonomy. If these dimensions are presented as length-height plots, there is a clear linear trend, although more measurements are necessary.

Figure 2. 6 : Length-height graph drawn using data in King (1968 MS)



A similar linear trend is seen in the present study; the following L/H graph was drawn for twenty-five specimens from the Beeston Chalk at Caistor St Edmunds